The Use of Birds as Biodiversity Indicators of Climatic Change: Downscaling European Indicators to Regional and National Trends

BELLAMY, CHARLOTTE,JANE

The Use of Birds as Biodiversity Indicators of Climatic Change: Downscaling European Indicators to Regional and National Trends

Charlotte Bellamy

School of Biological and Biomedical Sciences,

Durham University

2012

This thesis is submitted in candidature for the degree of

Master of Science

Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other University. The research reported within this thesis has been conducted by the author, unless indicated otherwise.

Abstract

This thesis examines the impacts of recent climatic change on bird species across Europe and develops robust indicators of ecosystem change at national and supra-national levels. The performance of three methods of species distribution modelling of European bird populations in relation to climatic change over the last 60 years is evaluated; the models being generalized additive models (GAM), climate response surface models (CRS) and maximum entropy models (MaxEnt). European breeding bird distributions were simulated using models that were parameterised using: (1) distribution data from the Climatic Atlas of European Breeding Birds and (2) augmenting these European data with distribution data from Turkey, Cyprus and North Africa. Including data from a wider geographical area improved the fit of SDMs; this was especially marked for some species with relatively poor fits based on the Europe-only dataset. Of the three SDM models tested CRS best simulated current species range data (mean AUC=0.982), closely followed by GAM (mean AUC=0.950), with MaxEnt performing worst (mean AUC=0.741).

The most robust of the modelling techniques (CRS and GAM) were used to produce climate suitability trends (CST) for European breeding birds, using population data provided by the Pan European Common Bird Monitoring Scheme (PECBMS). Population trends in European breeding birds significantly correlated with SDM retrodicted trends in 5 of 11 countries considered. Biological variables were assessed to examine their impacts on recent abundance trends; of these, habitat preference was the only biological variable found to impact upon the relationship between CST and the PECBMS trends. We generated indicators of the impact of climatic change by contrasting species trends of those projected to increase versus those projected to decline from the SDMs based on regional and national level data. Indices were also produced for individual species based on their observed and simulated trends among countries. Monitoring duration had a substantial effect on the strength of the indicator; therefore, the continuous updating of monitoring schemes is vital to ensure the accuracy of such indicators. Downscaling the continental indicator produced informative and reliable indicators that can inform policy decisions at a national level, helping to preserve biodiversity.

Acknowledgements

Throughout the work on this thesis I have received support from a number of people. I would like to thank Stephen Willis (primary supervisor), Phil Stephens, Richard Green and Rhys Gregory (co-supervisors) for their input and invaluable comments on my work. I could not have completed this work without continued help and support from Yvonne Collingham.

I would like to thank the Grevillea Trust for the Scholarship given to me which contributed towards my tuition fees and the Pan European Common Bird Monitoring Scheme for providing data used in this project. Finally, I would like to thank my family for their unconditional support and encouragement.

Contents

Figures and Tables:

Chapter 1- The Use of Birds as Biodiversity Indicators of Climatic change: Down-Scaling European Indicators to Sub-European and National Trends

Global climatic change is not a new phenomenon and has been documented in the past (Graham and Grimm 1990, Huntley *et al.* 1993). However, modern global climatic change is believed to be an anthropogenic occurrence (La Sorte and Jetz 2010). The Intergovernmental Panel on Climate Change (IPCC) define climatic change as, 'any change in the state of the climate that can be identified, whether due to natural variability or resulting from human activity' (IPCC 2007).

Copious evidence exists, both observational and empirical, documenting the extent and rate of climatic change. Over the past 100 years the global average temperature is estimated to have risen by 0.6°C (IPCC 2007, Root *et al.* 2003, Torti and Dunn 2005). During this time, two main warming periods have been identified: the first between 1910 and 1945 and the second from 1976 onward (Figure 1.1).

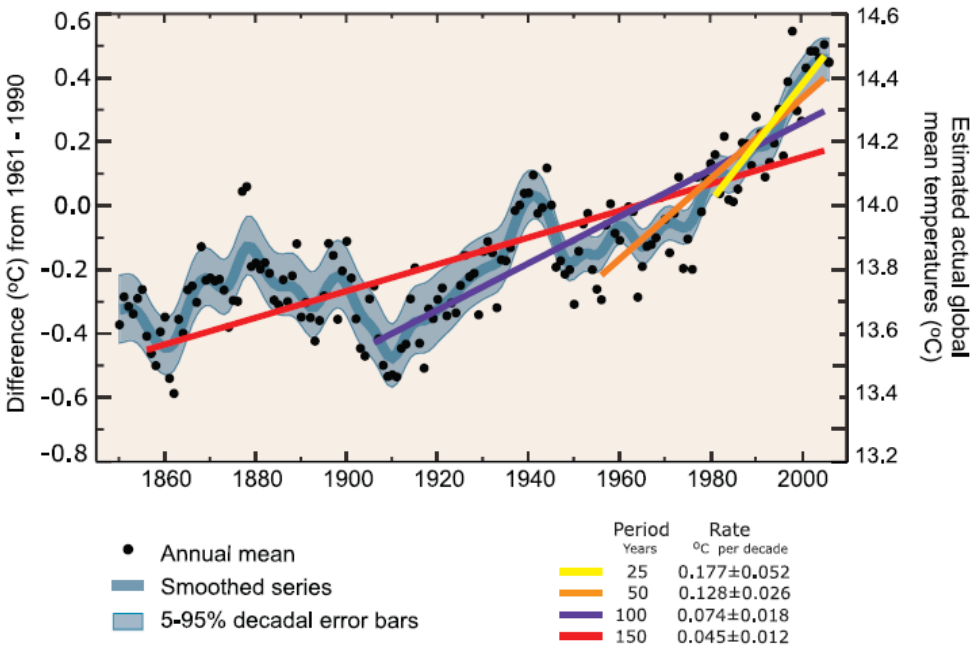


Figure 1.1 The trend in annual global mean temperatures from 1850 to the beginning of the 21st Century, indicating the recent sharp increase in global mean temperature. Black dots represent global mean temperatures with linear fits to the data. Linear trends are shown for the last 25 (yellow), 50 (orange), 100 (magenta) and 150 years (red). The smooth blue curve shows decadal variations, with the pale blue band about that line showing the decadal 90% error range. Temperature peaks before 1915 are accredited to naturally occurring climatic events. Temperature increases post 1915 are deemed to be due to anthropogenic disturbances such as industrialisation. From IPCC (2007) 253.

The temperature increase in the later twentieth century has been identified by the IPCC as the sharpest rise in temperature over the last century (Trenberth *et al.* 2007). Global climatic change is a measure of periodical changes in weather distribution and monitors variation in precipitation levels, humidity and extreme events. Each of these variables, coupled with human induced habitat fragmentation, can affect the resilience of an ecosystem to pressures such as pollution, invasive species, erosion and over-exploitation (European Commission 2009).

Climate influences a variety of ecological processes (Stenseth *et al.* 2002), affecting the ability of ecosystems to provide the services upon which economies and societies depend (EEA Technical report 2007, TEEB 2010). Levels of biodiversity throughout Western Europe are suggested to be affected by the two negative pressures of climatic change and land use change (Julliard *et al.* 2003). By reducing ecosystem functioning, climatic change is acting to reduce biodiversity (Leemans and Eickhout 2004). Biodiversity can be defined as 'The variety of life forms, the ecological roles they play and genetic diversity they contain' (Wilcox 1984). Climatic change is, therefore, considered a major threat to conservation (McCarty 2001) and a primary concern for the setting of conservation priorities (Jetz *et al.* 2007). The global importance of the effects of climatic change on levels of biodiversity is of great concern and has been recognised by policy makers who, in 2002, at the Convention on Biological Diversity, set a global target 'to achieve by 2010 a significant reduction of the current rate of biodiversity loss' (Mace and Baillie 2007). This target has since been missed by the majority of nations and replaced by a new suite of targets and goals for 2020 (Harrop 2011, Perrings *et al.* 2011). In order to measure progress towards targets set for conservation priorities, indicators of change are produced using species whose population changes reflect most closely those of biodiversity as a whole. The necessity of producing indicators which are as accurate as possible, to inform policy makers, has become even clearer since the failure of most nations to meet the 2010 targets of biodiversity loss reduction.

Many factors that affect the development of indicators must be considered. This chapter provides a necessary grounding and overview of some of the details of this research area. In this review I will first consider a number of ecological responses which species have developed to cope with the pressures of climatic change. I will then discuss the current predictions for the levels and rate of future climatic change. I will go on to

examine why birds are so often used as subject species in this area of research. Next I will provide an overview of the methods used to predict the effect of climatic change on species' distributions, as well as a discussion of how reliable the species distribution modelling is as a predictor of change. Finally I will consider the relevance of downscaling models and why this approach is necessary.

1.2 Ecological Responses to Climatic Change

Recent warming is strongly affecting terrestrial biological systems (IPCC 2007). Climatic change is currently impacting upon both species and ecosystems (McCarty 2001). Species will respond to climatic change in different ways at all levels of ecological organisation due to the complex nature of these responses through responses such as: shifts in geographical range and distribution patterns (Thomas and Lennon 1999, Cotton 2003, Hitch and Leberg 2007, Carey 2009, Doswald *et al.* 2009); phenological and life history adaptations (McCarty 2001, Peintinger and Schuster 2005, Torti and Dunn 2005, Sanderson *et al.* 2006); varying population size (Both and Visser 2001, Huntley *et al.* 2006, Husby *et al.* 2009, Saino *et al.* 2009); and extinctions (Sekerciolglu *et al.* 2008). These modifications result in a transformation of the composition, structure and function of ecosystems (McCarty 2001). Climatic change is having a detectable effect throughout European bird populations; those populations demonstrated to be negatively impacted (reducing populations) by climatic change are three times more frequent than populations that are positively affected (increasing populations) (Gregory *et al.* 2009). Much evidence exists documenting the occurrence of such changes both throughout plant and animal taxa, and specifically in species of bird (Thomas and Lennon 1999, Both and Visser 2001, Torti and Dunn 2005, Hitch and Leberg 2007, Carey 2009). These changes can be linked to observed population declines, and the local and global extinctions of species (McCarty 2001).

1.2.1 Changes in Distribution

Climate is an important determinant of geographic range for many species (McCarty 2001). The response to climatic change is expected to vary greatly between regions and species (Brown *et al.* 1999, Carey 2009). However, climate warming is known to be driving local extinctions of northern species (Franco *et al.* 2006); the bio-geographic response of many plant and animal species has been to shift poleward and upward to colonise higher latitudes and altitudes (Walther *et al.* 2002, Julliard *et al.* 2003, Beale *et al.* 2008, Carey 2009). Hickling *et al.* (2006) suggest these shifts are occurring at a rate of 12.5-19km decade^{-1} in the UK (Figure 1.2).

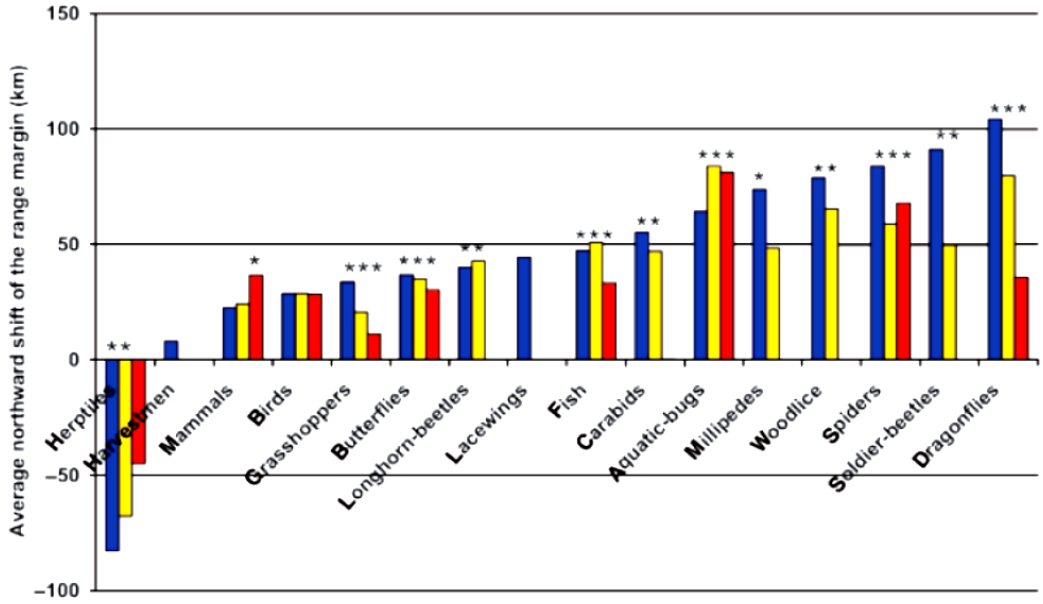


Figure 1.2 Latitudinal shifts in the northern range margins of 16 taxonomic groups in response to recent climatic change. The colour of the bar represents the level of sampling; Recorded=Blue, Well Recorded=Yellow, Heavily Recorded=Red and asterisks indicate significant range shifts (P<0.05). From Hickling *et al.* (2006).

Shifts in the geographic distribution of many taxonomic groups in response to climatic change are commonplace in the paleoclimatological record (Root *et al.* 2003, Carey 2009). However, although range shifts due to climatic change are not a new phenomenon (La Sorte and Jetz 2010), the rate at which the current climate is changing and the impact of anthropogenic habitat fragmentation limits the range shift responses available (Opdam and Wascher 2004). Many species may only be able to alter distribution in landscapes which provide sufficient habitat to allow expansion (Wilson *et al.* 2009); therefore land-use change by humans presents a further key pressure upon species in addition to climatic change. Honnay *et al.* (2002) found that species colonisation of forest plant species, at the northern boundary of their ranges, were

hampered due habitat fragmentation. This fragmentation induced dispersal limitation prevents habitat colonisation.

Shifts in the distribution of species during recent climatic change may be due to heat stress, physiological constraint, increased pathogen pressure or competition with colonising populations of more southerly species in increasingly species rich communities (Lemoine *et al.* 2007), or because the resource depended upon by a species has itself undergone a range shift in response to climatic change (Thomas *et al.* 2004, Hickling *et al.* 2006)

An analysis carried out using information from 143 studies of species trends over a time span of 34.5 years on average, looking at a wide variety of species (approximately 1,473 in total), suggested that over 80% of species are already undergoing range shifts in the expected direction (Root *et al.* 2003). Northward expansion has been observed in species of mammals, birds and butterflies (Both and Visser 2001, McCarty 2001). The extent of these expansions is suggested to be correlated with increasing temperatures; Franco *et al.* (2006) provide evidence that butterfly species range retreats are occurring at a rate which would be expected given the estimated 0.6°C rise in temperature. Alterations in species' geographic distributions can also result in perturbations of communities (Cotton 2003); for example, the northward expansion of the red fox (*Vulpes vulpes*) may enable this species to outcompete the more northerly arctic fox (*Alopex lagopus*) (McCarty 2001).

Changes in bird species' distributions towards cooler climes, i.e. northward and upward to higher altitudes, are a proposed indicator of recent climatic change. Many studies have found the northern limit of several species of bird to be affected by global temperature. Hitch and Leberg (2007) suggest that the northern limit of multiple bird species in North America, which have a naturally southern distribution, showed a significant shift northward of approximately 2.35km/yr on average. This research followed on from work carried out by Thomas and Lennon (1999) in Britain, who indicated that the northern margins of bird species in Britain were also shifting northward at an average rate of 0.945km/yr. Recent research has suggests that birds are now more than 200km behind the north-shifting climate zones (Devictor *et al.* 2012).

1.2.2 Phenological Adaptations to Climate Change

A further method of coping with climatic change is to adapt phenologically. Although this study is mainly concerned with changes in the breeding distribution of avian species, it is worth considering other recognised responses to climatic change to consider whether bird responses to climatic change are likely to be indicative of the responses of biodiversity as a whole. This is important when considering the use of birds to produce indicators of biodiversity.

Phenology refers to the study of events within an organism's life cycle, for example fertilisation, development and growth. These phenological events are not fixed in time and are often influenced by external cues (Visser *et al.* 2010). Phenological adaptations can involve shifts in seasonal biological events that are temperature driven such as the timing of flowering, leaf unfolding, migration and breeding (Cotton 2003, Strode 2003, IPCC 2007). The magnitude of such phenological adaptations is expected to vary regionally and by species. However, the adaptation of one species within a community, to climatic change, does not guarantee similar shifts in other species within that community. This can impact upon fine-tuned species interactions and have knock on effects on the persistence of ecological communities (Walther *et al.* 2001).

Recent climatic change has affected plants and animals worldwide. Many organisms have responded to increased spring temperatures by advancing dates of growth and reproduction, including amphibians which have been confirmed to breed earlier under the influence of recent climatic change (Parmesan 2006). The phenology of plants such as fruiting and flowering is highly sensitive to environmental cues such as temperature and moisture (Sherry *et al.* 2007). Comparison of satellite observations between now and the early 1980s reveal that warmer springs have lead to earlier 'greening' of vegetation in many regions (Lucht *et al.* 2002). This adaptation to climatic change is likely to cause a disruption of connectedness between species in current ecosystems (Root *et al.* 2003) which may, in turn, affect community level patterns of reproductive phenology (Sherry *et al.* 2007).

Recent climatic change has lead to mismatching in birds between timing of peak food supply and nestling demand, which severely impacts upon reproduction, shifting the optimal time for breeding (Carey 2009). Studies on blue tits (*Parus caeruleus*) have shown that climate induced mismatches between breeding and local productivity have

lead to increases in the costs involved with rearing offspring, this in turn reduces the persistence of adults in the breeding population (Thomas *et al.* 2001). The increase in spring temperature in temperate regions over the past 20 years has led to advancing tree phenology and, subsequently, earlier peaks in insect abundance (Both and Visser 2001). Several bird species have reacted, through selective forces, by adapting their phenology and advancing their laying date in response to this advancement in their food supply (Both and Visser 2001, Thomas *et al.* 2001, Weatherhead 2005). It is not only food supplies that are being affected; climatic change is also causing mismatches in snow cover and other factors that could severely impact successful migration and reproduction of avian populations, unless they are able to adjust to new conditions (Carey 2009).

Ample evidence exists of birds adapting to climatic change and advancing their laying date in response to long-term increases in spring temperature (Walther *et al.* 2002, Julliard *et al.* 2004, Strode 2003, Torti and Dunn 2005). Tree swallow (*Tachycineta bicolor*) breeding dates advanced by 5 - 9 days between the years 1959 and 1991; this advance in laying date was found to be correlated with local temperature rises (McCarty 2001). The advancement in the laying date of the Mexican Jay (*Aphelocoma ultramarina*) is correlated with climatic change variables including the amount of rain and the coldest temperature of the preceding winter (Brown *et al.* 1999). Many migratory species have, as a result, adapted the dates of their migration in order to prevent mismatching (Cotton 2003). An analysis of 17 migratory species in south western Germany revealed that, on average, these species were arriving 0.3 (max 2.9) days earlier per year between 1977 and 2003 (Peintinger and Schuster 2005). Antarctic migratory seabirds have been found to be arriving at breeding colonies 9.1 days later and laying eggs 2.1 days later, on average, than in the early 1950s. This has been linked with the decreasing sea ice in eastern Antarctica cause by global climatic change (Barbraud and Weimerskirch 2006). Other aspects of avian phenology which have been suggested to be influenced by climatic change include the number of double brooding females. Husby *et al.* (2009) suggest that this number has declined among great tit (*Parus major*) populations, in relation to the timing of the first clutch relative to peak caterpillar abundance. This indicates a possible shift in the life-history trait of this species in response to climatic change.

Not all species are able to adapt to climate-induced changes in peak food supply, indicating limitations in adaptive phenology. Both et al. (2006) uncovered a possible failure in phenological responses of the migratory pied flycatcher (*Ficedula hypoleuca*). The adjustment of breeding to an advanced food peak was found to be insufficient, resulting in an observed population decline of approximately 90% due to mistiming.

1.2.3 Decreasing Abundance and Extinctions

Species extinctions lead to changes in community composition. In wild animals and plants, climate-induced extinctions are being documented at an increasing rate (Easterling *et al.* 2000, Franco *et al.* 2006, Thomas *et al.* 2006, Devictor *et al.* 2008). Sekercioglu *et al.* (2008) forecast an increase in bird extinctions, in comparison to the current rate, of 100–500 species for every degree of projected warming.

Climatic change-induced temperature rises favour species with high optimal temperatures and disadvantage species with low optimal temperatures. Therefore, the more northerly is a species' distribution, the steeper its rate of decline due to factors such as heat stress and competition with colonising southerly species (Lemoine *et al.* 2007). Climatic change is purported to be the cause of recent rapid population declines observed in several species (Julliard *et al.* 2003).

The mismatches between timing of peak food supply and nestling demand, caused by recent climatic change, have severely impacted upon rates of extinction (Julliard *et al.* 2004, Carey 2009). Climatic change has been linked with a lifecycle disruption between the common cuckoo (*Cuculus canorus*) and its parasitic association with a number of its important host species. This mistiming is a likely contributor to the observed decline of cuckoo populations (Saino *et al.* 2009); however, Douglas *et al.* (2010) argue that the advancement in host breeding is not a primary driver of cuckoo decline in the UK. Population and species level extinctions have also been documented in frogs (Thomas *et al.* 2006). Recent rises in temperature have also led to substantial climate induced mortality in fish, at the scale of entire populations (Biro *et al.* 2007).

Specialist species appear to be declining at a much higher rate than generalist species (Julliard *et al.* 2003, van Turnhout *et al.* 2010). Specialist species, by their nature, rely on a specific food, habitat or shelter for survival (Dukes and Mooney 1999). This ecological specialisation is suggested to significantly impede the potential response of

species to environmental change, due to the restricted subset of resources available for utilisation, resulting in species decline and an increased risk of extinction (McKinney 1997, Fisher *et al*. 2003, Julliard *et al*. 2004, Biesmeijer *et al.* 2006,). This decline in specialist species, due to increased competition with generalist species for declining resources, will result in functional homogenisation of community-level biodiversity (Clavel *et al.* 2010).

Climatic variables such as the variability of precipitation can also increase the rates of extinction. Water stress is also a prime determinant of vegetation distribution; therefore, natural systems can change rapidly in response to precipitation. For example, variability of the timing of snow fall can hinder the feeding of grazing animals (McCarty 2001).

Despite the plentiful data on the negative responses of species to climatic change, positive impacts also exist. Leemans and Eickhout (2004) studied the possible adaptation of ecosystems and hypothesised that, if tundra is replaced by forests in response to climatic change, the resultant new forests have the potential to store more carbon and provide more ecosystem services, compared to tundra. Menendez *et al.* (2006) have also suggested that climatic change has, in some regions, enabled an increase in species richness. Increased temperature has enabled an increase in the abundance of species with range centres in Southern Europe, previously limited by low winter or spring temperature. Furthermore this temperature increase has increased juvenile survival rate and population density of birds in the United Kingdom (Lemoine *et al.* 2007). Climatic change may also act to mediate competition between short and long distance migrants and enhance overwintering survival of birds wintering in Europe. This, however, may lead to declines in migrant populations due to increased competition with short distance migrants (Sanderson *et al.* 2006, Doswald *et al.* 2009).

1.3 Future Climate Predictions

Many differing predictions of the rate and level of future climatic change have been made. Houghton *et al.* (2001) predict global average temperatures to increase at a rapid rate in the next 40 years and continue to rise for at least 100 years, at rates of 1.4-5.8°C, altering ecosystem function and resilience. Models of climatic change forecast northern latitude warming to exceed global mean warming by 40% (Strode 2003). By the 2080's the average national temperature across the United Kingdom may have risen by up to

3.5°C on average temperature data collected by Hulme *et al.* (2002). The Millennium Ecosystem Assessment, an international report launched by the United Nations to analyse the condition of the world's ecosystems and the services they provide, concludes that human activity is fundamentally changing the environment, leading to extinction on a massive scale (Millennium Ecosystem Assessment 2006). Future scenarios forecast that 400 species may be expected to suffer range reductions of over 50% by 2050 and that 950-1,800 species of land birds could be imperilled by climatic change and land conversions by 2100 (Jetz *et al.* 2007). By 2050 15-37% of existing plant and animal species are predicted to become extinct (Millennium Ecosystem Assessment 2006). If these predictions come to fruition the long-term survival of many northern and mountain species will be under threat (Franco *et al.* 2006) and many more species would be expected to advance their laying dates (Torti and Dunn 2005). Similarly, future distribution and abundance changes of many species would likely dwarf those already seen, threatening both species diversity and critical ecosystem services (Franco *et al.* 2006, McLaughlin *et al.* 2002). Although responses to climatic change discussed included adaptation and range shifts, the ability of ecosystems to adapt is predicted to be exceeded by climatic change and its associated disturbances (IPCC 2007). A warming of approximately 0.2°C per decade is projected for the next two decades under a range of SRES emissions scenarios (IPCC 2007). If this increase were to occur over 1000 years, most species would be expected to adapt; however, such a rapid increase is expected to lead to the swift deterioration of many ecosystems (Leemans and Eickhout 2004). Using mid-range climate-warming scenarios for 2050, Thomas *et al.* (2004) estimated that, in their sample of regions (covering 20% of the Earth's surface) and taxa (1,103 animal and plant species), 15–37% of these species will be 'committed to extinction'. This would result in major changes in ecosystem function and structure, ecological interactions and species' geographical ranges, producing primarily negative consequences for biodiversity and ecosystem services (IPCC 2007). Principally in interactions with other stressors such as habitat fragmentation (McCarty 2001), this may impede migration and gene flow (Carey 2009). Knowledge of past climatic variability and understanding how climate is changing in space and time are crucial for understanding and modelling current and future climate trends.

1.4 Why Birds Make Good Gauges of Ecosystem Health

It is widely acknowledged that there is a lack of basic systems in place to measure the progress of conservation actions in limiting biodiversity loss (Balmford *et al.* 2003, Green *et al.* 2005, Gregory *et al.* 2005). The use of indicator species, a form of surrogate species, provides a shortcut to monitor or solve conservation problems. Indicator species can be used to assess the magnitude of anthropogenic disturbance, as a proxy for ecosystem health and to monitor population trends in other species, providing a bridge between science and policy (Caro and O'Doherty 1999, Julliard *et al.* 2003, Gregory *et al.* 2005, Gregory *et al.* 2007).

Birds provide an excellent opportunity to study large scale effects of climatic change (Strode 2003) because their geographical ranges have been shown to be strongly associated with temperature, making them sensitive to environmental change (Hitch and Leberg 2007). In addition, birds make especially good barometers for the health of the environment for numerous reasons. They are easily identifiable taxa (Walther *et al.* 2002), with a well resolved taxonomy and moderate life span, that occur in many habitats. The level of understanding of their behaviour and population biology is exceptionally high (Gregory *et al.* 2005). Birds resonate with the public and are the focus of many volunteer monitoring schemes (Walther *et al.* 2002, EEA 2007) and considerable political concern (Julliard *et al.* 2003). Therefore a large amount of high quality, standardised, long-term data exists on past bird populations, and new data are relatively inexpensive to obtain (Gregory *et al.* 2005).

Many researchers do not agree with using a single species to model the health of entire ecosystems and to make projections concerning future biodiversity (Prenergast et al. 1993, Thomas *et al.* 2004). Hickling (2006) suggests that using a small selection of taxa may not be representative of biodiversity as a whole. However, it is widely suggested that bird diversity closely mirrors that of other taxa. For example, European studies have demonstrated a parallel decline of farmland birds with many insect, vertebrate and plant species, driven by agricultural intensification and specialisation (Gregory et al. 2005). Norris and Pain (2002) have suggested that there is often reasonable agreement in the relative richness of birds and other taxonomic groups (Figure 1.3). However, the use of multi-species indicators has been suggested as a disadvantageous technique because species with different generation times, habitat associations, dispersal

capacities or thermal physiologies might show very different responses to changing climate (Kullman 2002). The migratory habits of birds have also been suggested to make it difficult to link populations with specific drivers on the ground. Furthermore, using pre-calculated data may result in studies biased to particular taxa, habitat and regions (Mace and Baillie 2007). However, although no single metric is likely to describe adequately changes in biodiversity as a whole, birds provide a suitable surrogate for ecosystem health for use in this study (Gregory *et al.* 2005).

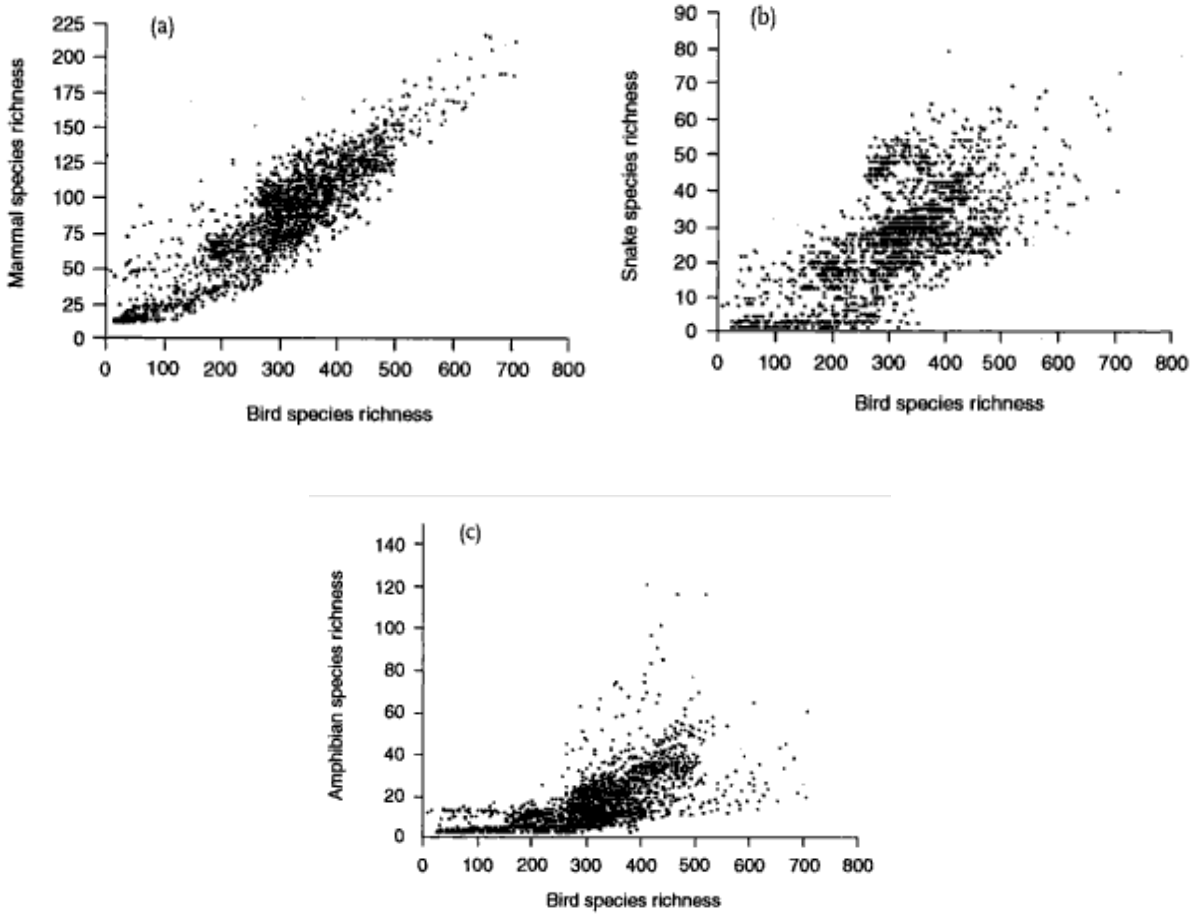


Figure 1.3 Varying continent-wide patterns of congruence in species richness across 1962 1° grid cells of sub-Saharan Africa. (a) Mammals vs. birds (r_s=0.84) (b) Snakes vs. birds (r_s=0.65) (c) Amphibians vs birds (r_s=0.69). From Norris and Pain (2002).

Indicator species are not a substitute for detailed knowledge of ecological process or individual species responses, which are essential in assessing the causes of change and in formulating strategies or plans in response to such changes (Bibby 1999, Gregory *et al.* 2005). However, indicator species are generally viewed as a potentially powerful tool to enable scientific information to be communicated to policy makers (Gregory *et al.* 2005).

Landres *et al.* (1988) give a definition of an indicator species as '*an organism whose characteristics (e.g. presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient or expensive to measure for other species or environmental conditions of interest.*' Global climatic change is well underway but our empirical knowledge of the biological consequences of this phenomenon remains confined primarily to species in well studied regions of the globe (La Sorte and Jetz 2010).

Climatic change indicators are used to monitor levels of biodiversity, assess whether biodiversity targets are met and both to quantify and to communicate these complex phenomena in a simple manner to inform policy decision makers (Gregory *et al.* 2005, Mace and Baillie 2007). Climatic change indicators are central to evaluating progress towards targets i.e. the 2010 biodiversity target (Gregory *et al*. 2005). Indicators have four basic functions: simplification, quantification, standardisation and communication. For an indicator to be effective it must meet certain criteria (EEA 2007). Indicators must be reliable, cost effective, relevant, and resonate with public audiences in order to inform policy decision makers, usefully contributing to conservation and biodiversity management (Mace and Baillie 2007). Using knowledge from extensive data sets, indicators enable the portrayal of ecosystem functions and broader benefits to society. This provides the possibility of reviewing policy in response to changes in an indicator (Julliard *et al.* 2003, Mace and Baillie 2007, Carey 2009) and can offer an indication of the possible outcomes of future climatic change (Graham and Grimm 1990).

Observed changes in the distribution of an indicator species can be modelled against climatic change over the same period. This enables the analysis of any links between climate and population trends. Applying predictions of future climatic changes to species' current distribution can further enable estimations of impending scenarios.

1.5 Species Distribution Models (SDMs)

Heikkinen *et al.* (2006) describe climatic envelope models (CEMs) as '*a type of species distribution model (SDM)... in which the biogeographical distributions of species are related to broad-scale variation in climate by given modelling techniques*'. CEMs are a statistical tool which can be used to carry out rapid analyses of the effects on biodiversity of potential climate warming (Pearson and Dawson 2003), by calculating

the response of species rather than communities (Graham *et al.* 1996). CEMs provide a descriptive characterisation of niche space (Beale *et al.* 2008) and seek to identify the climate 'envelope' that best explains the limits to a species' spatial range, by correlating the existing species distributions with chosen climate variables (Heikkinen *et al.* 2006, Thuiller 2003). Several different modelling techniques are used within the realm of climatic envelope modelling, a selection of which are discussed in more detail below. The reliability of predicted future species distributions depends strongly on the modelling technique used (Thuiller 2003). The SDMs selected for use in this research (CRS, GAM and MAXENT) are commonly used techniques in species distribution modelling and have been demonstrated to be capable of predicting current species distributions (Thuiller 2003, Araújo *et al.* 2005). SDMs can also be utilised to simulate potential future species' distributions, and population trends, under forecast climatic change scenarios (Heikkinen *et al.* 2006, Green *et al.* 2008) and project species at risk of extinction under future climatic change scenarios (Araújo *et al.* 2005). SDMs are frequently used to simulate potential impacts of future climatic change on the breeding ranges of birds (Doswald *et al.* 2009).

In the subsections below I briefly describe the modelling approaches adopted.

Climate Response Surface (CRS)

This model provides a convenient portrayal of the relationship between species distribution patterns and climate variables (Huntley *et al*. 1993). The model uses locally weighted regression (Cleveland and Devlin 1988) to fit the species' distribution to several pre-determined bioclimatic variables. CRS models are capable of predicting both past and potential future distributions of species through the application of different climate scenarios to enable the probability of species occurrence to be estimated. Studies into the performance of different indicators have suggested that CRS outperforms some rival modelling techniques such as generalised linear models (GLMs) and generalised additive models (GAMs) (Doswald *et al.* 2009), because they make no assumptions concerning the nature of the relationship between the probability of species occurrence and the bioclimatic variables used; instead, CRSs are able to mimic these interactions (Huntley *et al.* 2006, 2008).

In this research, three explanatory climate variables are used in both CRS and the two additional modelling approaches described below. These three climate variables have been found by other studies to map European bird species effectively (Huntley *et al.* 1995, 2006, 2008).

- Mean Temperature of Coldest Month (MTCO) – Measures the extremity of winter temperature.
- Growth Degree Days above 5°C (GDD5) – The annual sum of daily temperatures exceeding 5°C.
- Ratio of annual actual to potential evapotranspiration (AET/PET) – More informative than measures of precipitation levels, this variable reflects the amount of moisture available for organisms. Low values are produced when rates of evaporation are similar to those of precipitation.

Generalised Additive Models (GAMs)

GAMs are regression based techniques which use non-parametric smoothers to model non-linear trends between species presence (dependent variable) and environmental data (independent variable) (Hijmans and Graham 2006). This creates species response curves which are more accurately fitted to environmental gradients.

GAMs are a preferred climate envelope modelling technique as they are less sensitive to model over-fitting (Hijmans and Graham 2006). They are increasingly being utilised over the parametric general linear models (GLMs) (Thuiller 2003), due to their strong statistical foundation and realistic ability to model ecological relationships (Elith *et al.* 2006).

Maximum Entropy Models (MaxEnt)

MaxEnt models involve application of a machine learning technique called ‘maximum entropy’ to take incomplete information sets and make predictions (Hijmans and Graham 2006). Machine learning techniques are able to improve their performance over time, based on previous results (Elith *et al.* 2006). MaxEnt deals with presence only data and is able to estimate the likely presence of a species under novel combinations of climate space (Hijmans and Graham 2006, Phillips *et al.* 2006) by finding the distribution of maximum entropy (that closest to uniform) subject to the constraint that the predicted value of each environmental variable under this estimated distribution

matches it's empirical average (Elith *et al.* 2006, Philips *et al.* 2006). The output of MaxEnt, like GAMs, are values between 0 (low) and 1 (high). However, MaxEnt can occasionally produce some very large over-predictions (Hijmans and Graham 2006).

Prior to the introduction and validation of MaxEnt, genetic algorithm for set rule prediction (GARP) was widely used. However, it has been demonstrated that MaxEnt outperforms this modelling technique (Foley *et al.* 2010).

1.6 Reliability of Models

Accurate predictions of how species distributions shift in response to global climatic change are fundamental to the successful adaptation of conservation policy (Beale *et al.* 2008). There is a great need to validate models relating species to climate due to significant variability among model predictions (Araújo *et al.* 2005). Different SDM techniques have been demonstrated to provide very different results for data sets of the same species and to vary widely across species (Thuiller 2003). A possible way of overcoming this is to use 'ensemble forecasting'. This involves the use of several models in one study and examining the results in a way which enables combination of each of the model outcomes (Araújo *et al.* 2005, Araújo and New 2007).

The simplicity of SDMs has led to their popularity but also to extensive criticism. The exclusion of mechanistic details in distribution models prevents SDM results from being overly informative (La Sorte and Jetz 2010) and often produces results that are loaded with ambiguity (Dormann *et al.* 2008). Problems exist in determining a causal relationship between climatic change, species distribution and extinction, because multiple environmental variables are likely to interact (Carey 2009). Independent evaluations of climate envelope models have been unable to demonstrate or agree upon the pre-eminence of any single model (Ajaúro and New 2007). Therefore, there is a lack of general consensus upon which of all the available modelling approaches provides the best insights (Jetz *et al.* 2007). As SDMs take into account the influences of biotic interactions upon communities, this relies upon the same interactions existing in future modelled communities, which may not be the case due to climatic change (Morin and Lechowicz 2008). Beale *et al.* (2008) carried out a quantitative assessment of the degree to which SDMs are fit for purpose and suggested that climatic envelope model results are no better than those which would be produced by chance for 68 of 100 European

bird species. This paper has, however, been highly criticised: Araújo *et al.* (2009) repeated the study using a more complete data set than *Beale et al.* (2008) and demonstrated improved model performance, with species-climate associations better than expected by chance. Land-use and ability to shift range between predicted distributions can also greatly affect the accuracy of SDMs (Dormann *et al.* 2008), as can the relative spread of species' distribution. Those species which are patchily distributed throughout a large region, when modelled, will generate results with a large margin of error. These factors all affect the predictive power of SDMs (Kadmon *et al.* 2003).

SDMs are more widely utilized than alternative approaches, such as physiological models which model fundamental niche rather than species' realised niche. As SDMs are relevant to many spatial scales and ecological niches, they are applicable to a wide range of species (Morin and Lechowicz 2008). Numerous studies have demonstrated the possible benefits of using SDMs. The most common method of validating SDMs is to use retrodiction of distribution changes to study the effects of climatic change. This has been carried out with CRS models (Green *et al.* 2008). The performance of SDMs must be tested to address these concerns concerning their levels of accuracy (Gregory *et al.* 2009). However, care must be taken when carrying out resubstitution studies to ensure that the model is not being validated by the same data used to calibrate it (Araújo *et al.* 2005). Luoto *et al.* (2007) suggest that the accuracy of SDMs over alternative modelling approaches is clearer when used at finer resolutions. Furthermore, recent SDM improvements have resulted in an enhanced ability to simulate extremes and many other aspects of climate variability (Easterling *et al.* 2000).

1.7 Downscaling Models

This thesis aims to downscale indicators in order to examine more closely the predicted changes in range and abundance of birds by the selected models, as an indicator of biodiversity in relation to climatic change and suitability. Europe consists of an extremely varied range of habitats and microclimates. Therefore, producing indicators at the scale of countries and sub-European regions may prove to be important, as pan-European indices are capable of masking a large amount of inter-country variation (Gregory *et al.* 2009). The relative importance of the threat of climatic change to biodiversity varies widely across biogeographical regions (EEA 2007). Species and communities do not respond to global average climatic change, but rather to regional

spatially heterogeneous changes (Torti and Dunn 2005). It has been demonstrated that, at a small spatial scale, temperature changes may differ substantially from the global average. Furthermore, asymmetry of changes in the precipitation regime may not be spatially or temporally uniform (Walther *et al.* 2002, Torti and Dunn 2005). For example, a review of 109 species found that phenological shifts were stronger north of 50°, where temperatures had warmed more than at lower latitudes over the past 50 years (Root *et al.* 2003).

1.8 Conclusion

Climatic change is already having widespread effects upon the biodiversity of ecosystems, through range shifts, phenological adaptation and extinction. Global climatic change is expected to continue; therefore the impact upon biodiversity will increase. Many studies have predicted responses of species to climatic change and have discussed changes already occurring due to climatic change. However, knowledge of smaller scale, national trends is limited for larger groups of species. The scale of response to climatic change is dependent upon many distinct, individualistic factors; these include the heterogeneous changes in temperature and precipitation, habitat and the population and species concerned. Therefore, investigating the effects of climatic change at sub-European levels can enable a more accurate monitoring of regional ecosystem biodiversity and a more robust indication of how climatic change is affecting global biodiversity. This thesis is concerned with addressing whether or not indicators downscaled to this level can still be informative and relied upon.

SDMs must be validated to ensure accurate indicators are produced. This in turn will ensure that, when considered by policy makers, these indicators may enable the protection of species and entire ecosystems from the imminent progression of climatic change. A great deal of research has been carried out using birds as biodiversity indicators and many attributes of birds make them an informative indicator for studies of the effects of climatic change. Species distribution models will be used in this work to relate the abundance of bird species to climate suitability. Analyses of different available SDM techniques (CRS, GAM, MaxEnt) are an important precursor to this work, because these SDMs will be used to create indicators at a smaller scale. Although SDMs have many issues associated with their accuracy and validity, they remain the most reliable tool at our disposal and can provide valuable predictions of species'

responses to climate. We must, however, remain mindful of the caveats of these methods.

Following this review of climatic change and the use of indicators to monitor species' responses to that change, it is possible to identify a number of objectives that will form the structure of the rest of this thesis. The main objective of this work is to explore the need for, and development of, robust indicators of climatic change using population trends of European breeding birds to predict the impact of climatic change upon ecosystem biodiversity at national and regional levels. To achieve this, the performance of the selected SDMs must first be examined. To ensure any indicators subsequently produced using these models are as accurate as possible, the most robust of these SDM will be used to develop climatic suitability trends (CST) (measure of species' mean probability of occurrence) through a comparison between SDM retrodicted trends and population data from the same period. This precursory work will then be brought together to produce indicators of the impact of climatic change which will be explored at downscaled national, regional and individual species' trend levels, the main crux of this work. Throughout this thesis the impact of additional biological and monitoring variables is considered in an attempt to validate the responses revealed by this investigation.

1.9 References

Araújo, M.B., Pearson, R.G., Thuiller, W. and Erhard, M. (2005) Validation of species-climate impact models under climate change. *Global Change Biology* **11** 1504-1513

Araújo, M.B. and New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution* **22** 42-47

Araújo, M.B., Thuiller, W. and Yoccoz, N.G. (2009) Reopening the climate envelope reveals macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences* **106** E45-E46

Balmford, A., Bennun, L., Ten Brink, B., Cooper, D., Cote, I.M., Crane, P., Dobson, A., Dudley, N., Dutton, I., Green, R.E., Gregory, R.D., Harrison, J., Kennedy, E.T., Kremen, C., Leader-Williams, N., Lovejoy, T.E., Mace, G., May, R., Mayaux, P., Morling, P., Phillips, J., Redford, K., Ricketts, T.H., Rodriguez, J.P.,

Sanjayan, M., Schei, P.J., van Jaarsveld, A.S. and Walther, B.A. (2005) The convention on biological diversity's 2010 target. *Science* **307** 212-213

Barbraud, C., and Weimerskirch, H. (2006) Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Sciences* **103** 6248-6251

Beale, C.M., Lennon, J.J. and Gimona, A. (2008) Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences* **105** 14908-14912

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R.,Thomas, C.D., Settele, J. and Kunin, W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313** 351–354

Both, C. and Visser, M.E. (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411** 296-298

Both, C., Bouwhuis, S., Lessells, C.M., and Visser, M.E. (2006) Climate change and population declines in a long-distance migratory bird. *Nature* **441** 81-83

Brown, J.L., Li, S-H. and Bhagabati, N. (1999) Long-tern trend toward earlier breeding in an American bird: A response to global warming? *Proceedings of the National Academy of Sciences* **96** 5565-5569

Carey, C. (2009) The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364** 3321-3330.

Caro, T.M. and O'Doherty (1999) On the use of surrogate species in conservation biology. *Conservation Biology* **13** 805-814

Clavel, J., Juilliard, R. and Devictor, V. (2010) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* **9** 222-228

Cleveland, W.S. and Devlin, S.J. (1988) Locally-weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association* **83** 596-610

Cotton, P.A. (2003) Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences* **100** 12219-12222

Devictor, V., Julliard, R., Couvet, D. and Jiguet, F. (2008) Birds are tracking climate warming, but not fast enough. *Proceedings of The Royal Society B Biological Sciences* **275** 2743-2748

Devictor, V., van Swaay, C., Brereton, T., Brontons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Ă., Reif, J., Roy, David., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I. and Jiguet, F. (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change* **2** 121-124

Dormann, C.F., Schweiger, O., Arens, P., Augenstein, I., Aviron, S., Bailey, D., Baudry, J., Billeter, R., Bugter, R., Bukácek, R., Burel, F., Cerny, M., De Cock, R., De Blust, G., DeFilippi, R., Diekötter, T., Dirksen, J., Durka, W., Edwards, P.J., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Liira, J., Maelfait, J.P., Opdam, P., Roubalova , M., Schermann-Legionnet, A., Schermann, N., Schmidt, T., Smulders, M.J.M., Speelmans, M., Simova, P., Verboom, J., van Wingerden, W. and Zobel, W. (2008) Prediction uncertainty of environmental change effects on temperate European biodiversity. *Ecology Letters* **11** 235-244

Doswald, N., Willis, S.G., Collingham, Y.C., Pain, D.J., Green, R.E. and Huntley, B. (2009) Potential impacts of climatic change on the breeding and non-breeding ranges and migration distance of European *Sylvia* warblers. *Journal of Biogeography* **36** 1194-1208

Douglas, D.J.T., Newson, S.E., Leech, D.L., Noble, D.G. and Robinson, R.A. (2010) How important are climate-induced changes in host availability for population processes in an obligate brood parasite, the European cuckoo? *Oikos* **119** 1834-1840

Dukes, J.S. and Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology & Evolution* **14** 135-139

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. and Mearns, L.O. (2000) Climate extremes: observations, modelling, and impacts. *Science* **289** 2068-2074

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira. R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S. and Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29** 129-151

Elith, J., Leathwick, J.R. and Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology* **77** 802-813

European Environment Agency (EEA) Technical report (2007). Halting the loss of biodiversity by 2010: proposal for a first set of indicators to monitor progress in Europe. EEA Copenhagen Section **1**

Fisher, D,O., Blomberg, S.P. and Owens, I.P.F. (2003) Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proceedings of the Royal Society London* **270** 1801–1808

Foley, D.H., Klein, T.A., Kim, H.C., Brown, T., Wilkerson, R.C. and Rueda, L.M. (2010) Validation of ecological niche models for potential malaria vectors in the Republic of Korea. *Journal of the American Mosquito Control Association* **26** 210-213

Franco, A.M.A., Hill, J.K., Kitschke, C., Collingham, Y.C., Roy, D.B., Fox, R.R., Huntley, B. and Thomas, C.D. (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* **12** 1545-1553

Graham, R.W. and Grimm, E.C. (1990) Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology and Evolution* **5** 289-292

Graham, R.W., Lundelius, E.L., Graham, M.A., Schroeder, E.K., Toomey, R.S., Anderson, E., Barnosky, A.D., Burns, J.A., Churcher, C.S., Grayson, D.K., Guthrie, R.D., Harington, C.R., Jefferson, G.T., Martin, L.D., McDonald, H.G., Morlan, R.E., Semken, H.A., Webb, S.D., Werdelin, L. and Wilson, M.C. (1996) Spatial responses of mammals to late quaternary environmental fluctuations. *Science* **272** 1601-1606

Green, R.E., Balmford, A.P., Crane, P.R., Mace, G.M., Reynolds, J.D. and Turner, R.K. (2005) A framework for improved monitoring of biodiversity: responses to the world summit on sustainable development. *Conservation Biology* **19** 56–65

Green, R.E., Collingham, Y.C., Willis, S.G., Gregory, R.D., Smith, K.W. and Huntley, B. (2008) Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters* **4** 599-602

Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B. and Gibbons, D.W. (2005) Developing indicators for European birds.

Philosophical Transactions of the Royal Society B: Biological Sciences **360** 269-288

Gregory, R.D., Vorisek, P., Strien, A.V., Meyling, A.W.G., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P. and Burfield, I.J. (2007) Population trends of widespread woodland birds in Europe. *Ibis* **149** 78-97

Harrop, S. R. (2011) 'Living in harmony with nature'? Outcomes of the 2010 Nagoya conference of the convention on biological diversity. *Journal of Environmental Law* **23** 117-128

Heikkinen, R.K., Luoto, M. and Virkkala, R. (2006) Does seasonal fine-tuning of climatic variables improve the performance of bioclimatic envelope models for migratory birds? *Diversity and Distributions* **12** 502-510

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. and Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12** 450-455

Hijmans, R.J. and Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* **12** 2272-2281

Hitch, A.T. and Leberg, P.L. (2007) Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology* **21** 534-539

Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B. and Hermy, M. (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters* **5** 525-530

Houghton, J.T., Callander, B.A. and Varney S.K. (eds) in *Climate change 2001: the science of climate change* Cambridge University Press, New York

Hulme, M., Jenkins, G.J., Lu, X., Turnpenny, J.R., Mitchell, T.D., Jones, R.G., Lowe, J., Murphy, J.M., Hassell, D., Boorman, P., McDonald, R. and Hill, S. (2002) *Climate change scenarios for the United Kingdom: The UKCIP02 scientific report.* Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich, UK 120

Huntley, B. (1993) Rapid early-Holocene migration and high abundance of hazel (*Corylus avellana* L.): Alternative hypotheses, 205-216 *IN* Chambers, F.M. *Climate change and human impact on the landscape.* Chapman and Hall, London

Huntley, B., Berry, P.M., Cramer, W. and McDonald, A.P. (1995) Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography* **22** 967-1001

Huntley, B., Collingham, Y.C., Green, R.E., Hilton, G.M., Rahbek, C. and Willis, S.G. (2006) Potential impacts of climatic change upon geographical distributions of birds. *Ibis* **148** 8-28

Huntley, B., Collingham, Y.C., Willis, S.G. and Green, R.E. (2008) Potential impacts of climate change on European breeding birds. *PLoS One* **3** 1439

Husby, A., Kruuk, L.E.B. and Visser, M.E. (2009) Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. *Philosophical Transactions of the Royal Society B: Biological Sciences* **276** 1845-1854

IPCC (2007) Climate change 2007: synthesis report. Contribution of working groups I, II and III to the Fourth Assessment. *Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]. IPCC, Geneva, Switzerland, 104

Jetz, W., Wilcove, D.S. and Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS One* **5** 1210-1219

Julliard, R., Jiguet, F. and Couvet, D. (2003) Common birds facing global changes: what makes a species at risk? *Global Change Biology* **10** 148-154

Julliard R, Jiguet F, and Couvet D. (2004) Evidence for the impact of global warming on the long-term population dynamics of common birds. *Proceedings of the Royal Society London* **271** 490–92

Kadmon, R., Farber, O. and Danin, A. (2003) A systematic analysis of factors affecting the performance of climatic envelope models. *Ecological Applications* **13** 853-867

Kullman, L. (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology* **90** 68-77

La Sorte, F.A. and Jetz, W. (2010) Avian distributions under climate change: towards improved projections. *The Journal of Experimental Biology* **213** 862-869

Landres, P.B., Verner, J. and Thomas, J.W. (1988) Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* **2** 316-328

Leemans, R. and Eickhout, B. (2004) Another reason for concern: regional and global impacts on ecosystems for different levels of climate change. *Global Environmental Change Part A* **14** 219-228

Lemoine, N., Bauer, H-G., Peintinger, M. and Böhning-Gaese, K. (2007) Effects of climate and land-use change on species abundance in a central European bird community. *Conservation Biology* **21** 495-503

Lucht, W., Prentice, C., Myeni, R.B., Sitch, S., Friedlingstein, P., Cramer, W., Bousquet, P., Buermann, W. and Smith, B. (2002) Climatic control of the high-latitude vegetation greening trend and Pinatubo effect. *Science* **296** 1687-1689

Luoto, M., Virkkala, R., and Heikkinen, R.K. (2007) The role of land cover in bioclimatic models depends on spatial resolution. *Global Ecology and Biogeography* **16** 34-42

Mace, G.M. and Baillie, J.E.M. (2007) The 2010 biodiversity indicators: challenges for science and policy. *Conservation Biology* **21** 1406-1413.

McCarty, J.P. (2001) Ecological consequences of recent climate change. *Conservation Biology* **15** 320-331

McKinney, M. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecological Systems **28** 495–516

McLaughlin, J.F., Hellmann, J.J., Boggs, C.L. and Ehrlich, P.R. (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences* **99** 6070-6074

Menéndez, R., Megías, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R. and Thomas, C.D. (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society B: Biological Sciences* **273** 1465-1470

Morin, X. and Lechowicz, M.J. (2008) Contemporary perspectives on the niche that can improve models of species range shifts under climate change. *Biology Letters* **4** 573-576

Opdam, P. and Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* **117** 285-297

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* **37** 637-669

Pearson, R.G. and Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12** 361-371

Peintinger, M. and Schuster, S. (2005) Changes in first arrival dates of common migratory bird species in southwestern Germany. *Vogelwarte* **43** 161–169

Perrings, C., Naeem, S., Ahrestani, F.S., Bunker, D.E., Burkill, P., Canziani, G., Elmqvist, T., Fuhrman, J.A., Jaksic, F.M., Kawabata, Z., Kinzig, A., Mace, G.M., Mooney, H., Prieur-Richard, A., Tschirhart, J. and Weisser, W. (2011) Ecosystem services, targets, and indicators for the conservation and sustainable use of biodiversity. *Frontiers in Ecology and the Environment* **9** 512–520

Phillips, S.J., Anderson, R.P. and Schapire, R.E. (2006) Maximum entropy modelling of species geographic distributions. *Ecological Modelling* **190** 231-259

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. and Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421** 57-60

Saino, N., Rubolini, D., Lehikoinen, E., Sokolov, L.V., Bonisoli-Alquati, A., Ambrosini, R., Boncoraglio, G. and Møller, A.P. (2009) Climate change effects on migration phenology may mismatch brood parasitic cuckoos and their hosts. *Biology Letters* **5** 539-541

Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. and van Bommel, F.P.J. (2006) Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation* **131** 93-105

Sekercioglu, C.H., Schneider, S.H., Fay, J.P. and Loarie, S.R. (2008) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* **22** 140-150

Sherry, R.A., Zhou, X., Gu, S., Arnone III, J.A., Schimel, D.S., Verburg, P.S., Wallace, L.L. and Luo, Y. (2007) Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences* **104** 198-202

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K-S. and Lima, M. (2002) Review: ecological effects of climate fluctuations. *Science* **297** 1292-1296

Strode, P.K. (2003) Implications of climate change for North American wood warblers (Parulidae). *Global Change Biology* **9** 1137-1144

TEEB (2010) Mainstreaming the economics of nature: a synthesis of the approach, conclusions and recommendations of TEEB

Thomas, C.D. and Lennon, J.J. (1999) Birds extend their ranges northwards. *Nature* **399** 213

Thomas, D.W., Blondel, J., Perret, P., Lambrechts, M.M. and Speakman, J.R. (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* **291** 2598-2600

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. and Williams, S.E. (2004). Extinction risk from climate change. *Nature* **427** 145-148

Thomas, C.D., Franco, A.M.A, and Hill, J.K. (2006) Range retractions and extinction in the face of climate warming. *TRENDS in Ecology and Evolution* **21** 415-416

Thuiller, W. (2003) BIOMOD- optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology* **9** 1353-1362

Torti, V.M. and Dunn, P.O. (2005) Variable effects of climate change on six species of North American birds. *Oecologia* **145** 486-495.

Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Klein Tank, A., Parker, D., Rahimzadeh, F., Renwick, J.A., Rusticucci, M., Soden O. and Zhai P., (2007). *Observations: surface and atmospheric climate change.* In: Climate change 2007: the physical science basis. Contribution of working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L. (eds.)]. *Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA* 235-336

van Turnhout, C.A.M., Foppen, R.P.B., Leuven, R.S.E.W., van Strien, A. and Siepel, H. (2010) Life-history and ecological correlates of population change in Dutch breeding birds. *Biological Conservation* **143** 173–181

Visser, M.E., Caro, S.P., van Oers, K., Schaper S.V. and Helm, B. (2010) Phenology, seasonal timing and circannial rhythms: towards a unified framework. *Philosophical transactions of the Royal Society B: Biological Sciences* **365** 3113-3127

Walther, G-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J-M., Hoegh-Guldberg, O. and Bairlein, F. (2002) Ecological responses to recent climate change. *Nature* **416** 389-395

Wilcox, B. A. (1984) In situ conservation of genetic resources: determinants of minimum area requirements. *In National Parks, Conservation and Development, Proceedings of the World Congress on National Parks, J.A. McNeely and K.R. Miller*, Smithsonian Institution Press, 18-30.

Weatherhead, P.J. (2005) Effects of climate variation on timing of nesting, reproductive success and offspring sex ratios of red-winged blackbirds. *Oecologia* **144** 168-175

Wilson, R.J., Davies, Z.G. and Thomas, C.D. (2009) Modelling the effect of habitat fragmentation on range expansion in a butterfly. *Proceedings of the Royal Society B: Biological Sciences* **276** 1421-1427

The UN Millennium Ecosystem Assessment (2006), House of Commons Environmental Audit Committee, Published 3 January 2007 House of Commons London: The Stationery Office Limited. http://www.publications.parliament.uk/pa/cm200607/cmselect/cmenvaud/77/77.pdf Accessed 25/11/2010

European Commission (2009), *Nature and Biodiversity*. Nature's role in climate change http://ec.europa.eu/environment/nature/info/pubs/docs/climate_change/en.pdf Accessed 27/11/2010

Chapter 2 –Species Distribution Models: Model Selection and Model Performance

2.1 Introduction

This chapter forms an important pre-cursory study to validate the use of the proposed datasets and species distribution models (SDMs) used to calculate climate suitability trends (CST) and, subsequently, to develop indicators. This initial investigation is crucial to understand the relationship between climate and bird distribution through Europe and to produce accurate climatic change indicators using available data and widely utilised SDMs, which forms the main exploratory work covered by this thesis.

The terms 'species distribution' and 'range' refer to the spatial arrangement of species occurrence. SDMs have been introduced previously; they are empirical models which relate recorded occurrence of species to environmental predictor variables, based on statistically, or theoretically, derived response surfaces (Guisan & Zimmermann 2000). This statistical procedure relates the response variable of a species distribution to environmental variables, estimating the relationship between species records at sites and the environmental and spatial characteristics of those sites (Franklin 2009). SDM models can be applied to novel climate scenarios to project the likelihood of a species' occurrence under that scenario, based on an assumption of close correlation between climate and the species distribution. Here, I model the relationship between the distribution of breeding birds in Europe and bioclimatic variables selected to represent the climate of the region.

Climatic change has been suggested by many previous studies to be a driver of population change and, more commonly, population declines, as discussed in Chapter 1 (Thomas and Lennon 1999, Both and Visser 2001, Torti and Dunn 2005, Hitch and Leberg 2007, Carey 2009). SDMs suffer from a number of limitations (see 1.1.6), predominantly arising from the assumption of a direct association between a species and climate, ignoring important biological parameters that could limit response to climatic change. Nonetheless, when correctly and cautiously interpreted, they provide the best means of inferring potential implications of future climate change on biodiversity (Guisan and Thuiller 2005). SDMs can be used to tackle many issues in conservation biology and applied ecology. SDMs rely upon the species niche concept as a central

theme (Guisan & Zimmermann 2000). Niche is defined as an area in which a species can potentially live (Grinnell, 1917). Hutchinson (1957), one of the pioneers of the niche concept, further distinguished Grinell's view of niche by the conception of the fundamental niche. The fundamental niche is the area of environmental space in which a species can live (i.e. occupying all suitable habitat), and the realised niche is the area within the fundamental niche which is actually occupied by the species as a result of biotic interactions (Silvertown 2004, Guisan and Thuiller 2005). It is suggested that, as observed distributions are already constrained by biotic interactions and limiting resources, SDMs are modelling the realised niches of species (Guisan and Thuiller 2005). Through SDMs, species' realised niche is depicted, by intersecting observed species' presence and absence data with environmental predictor variables.

No question in spatial ecology can be answered without referring explicitly to how data are measured or analysed (Wiens 2002). Careful consideration of data quality must be made to ensure successful predictions are produced by the analysis (Guisan and Zimmermann 2000) and, therefore, the most appropriate data used for further analysis. Small sample sizes have been shown to be a significant source of instability and error in models (Guisan and Thuiller 2005). The availability of high quality species distribution data is a key constraint when conducting regional studies across entire taxa (Hole *et al.* 2009). Although collecting new data is costly (Hirzel and Guisan 2002), data in non-digital form are sometimes available and require only digitisation to be included in SDMs.

SDMs are useful if they are robust (Guisan and Thuiller 2005). For example, addressing ecological questions with a model that is statistically significant, but only explains a low proportion of variance might lead to weak and possibly erroneous, conclusions (Mac-Nally 2002). This chapter provides an essential foundation to producing Climate Suitability Trends (CSTs); specifically, it is necessary in order to define the most appropriate modelling techniques and data sets, and to provide a summary of the models used throughout this work.

Previous work (Huntley *et al.* 2008, Araujo *et al.* 2011) demonstrated a 'good' fit for SDMs projecting species ranges of breeding birds across Europe using bioclimatic data for the region. However, these models did not include the southern range margins of a number of species whose ranges extended into North Africa. We might expect that

including such additional data on suitable and unsuitable climates would be expected to improve SDM predictions, for both the present climates and for future projections.

In this chapter, I explore two factors that have been shown to influence model performance of SDMs, to refine models that are used to produce CSTs in subsequent chapters. Firstly, I explore the ability of SDMs that include or exclude additional distribution and climate data beyond Europe to predict the current distribution of European breeding birds. Secondly, I assess the influence of these additional data on projections of future species richness of these species under climatic change. Thirdly, I explore the predictive ability of three contrasting modelling approaches.

2.2 Methods

2.2.1 Performance of SDM Using Additional Species Presence/Absence Data

The aim of this section is to determine whether, and to what extent, including the southern and south eastern range boundaries of European breeding bird species whose range spreads beyond Europe improves the performance of SDMs.

To assess whether the addition of extra-European range and climate data for European breeding birds improves the predictive ability of SDMs, we use a modelling approach that has been used previously to create SDMs for European breeding birds: Climate Response Surface modelling (CRS; Huntley et al. 2007), using Europe-only data. We directly compare the performance of the models excluding Turkey, Cyprus and North Africa, to those including these areas, to determine which best predicts species distributions and, therefore, which dataset should be used to calculate CST.

Species Distributions

Species distribution data included presence, absence and areas with no records. The breeding bird distribution data for 496 European species, collated by the European Breeding Bird Council (EBCC), was used to represent breeding bird distributions over Europe (excluding Turkey, Cyprus and North Africa). These data were collected principally during the years 1985-8 and record the presence or absence of recorded breeding by each species in a total of 4757 grid squares, each cell being approximately half degree (lat-long) resolution (approximately 50km x 50km) (Hagemeijer and Blair 1997). Records of ‘confirmed and probable breeding’ and ‘possible breeding’ were used

to indicate the presence of a species. These data distinguish between species absences (species were sought but not found) and grid cells where no data were received for a species.

Presence/absence data from North Africa were added using range polygon data made available from BirdLife International (www.birdlife.org/datazone/info/spcdownload) and gridded at a half degree resolution, to correspond to EBCC gridded data for Europe. Data from individual countries cover different time periods, as would be expected. The presence/absence data from North Africa were collected from between 1980 and 2000. This time period is approximately comparable to the European data. Cyprus distribution data were digitised from Snow and Perrins, (1998) and Turkey distribution data from Roselarr (2000); both gridded at a half degree resolution. The addition of this presence and absence data brings the total number of grid squares in which species data is recorded to 7830.

Bioclimatic Variables

The concept of the 'climatic normal' is used in this study (Arguez and Vose 2011). This measurement is the mean of the values recorded year by year for a period of 30 years. These data were taken from data provided by CRU TS 3.1 (badc.nerc.ac.uk). Here, data from the climatic normal period 1961-1990 has been used on the same half-degree grid as the species distribution data, and reflects the mean climate for the 30-year period preceding the collection of the species distribution data. Climatic data is from the global compilation by New *et al.* (1999), which interpolates meteorological station data to provide climatic conditions for all points of this grid. To compare the effect of adding extra-European data, we adopted the same bioclimatic variables used by Huntley et al. (2007) and the same modelling approach (CRS – see below for details). The predictor variables (environmental variables) used in this study are taken from a selection of studies where predictor variables have been tested and the 'best ones' determined. Huntley *et al.* (2007) suggest the use of GDD5, MTCO and AET/PET as these reflect the three main types of influence on species: limiting factors, disturbances and resources (Guisan and Zimmermann 2000) (discussed in more detail in section 2.2.1).

The bioclimatic variables used are as follows:

Annual temperature sum above 5°C (GDD5: degree days): This variable is a measure of overall warmth throughout the growing season. The cut off of 5°C is used as temperate plants usually have a threshold temperature for growth around this level (Sakamoto *et al* 1977). GDD5 is selected over the alternatives of absolute maximum annual temperature and mean temperature of the warmest month as it reflects the thermal sum, rather than the summer temperature extremes, that determines whether organisms can complete their annual growth and reproductive cycle at any given location. Species' northern limits in Europe more frequently align with GDD5 isolines than with isotherms for summer temperature (Williams 1986).

Mean temperature of the coldest month (MTCO: °C): This variable provides a measure of winter cold. This is used in preference to absolute minimum temperature principally as global compilations of absolute minimum annual temperature include fewer data points. However these two variables are highly correlated (Müller 1982; Prentice *et al.* 1992) and many species are known to be sensitive to low temperatures.

Annual ratio of actual to potential evapotranspiration (AET/PET): This variable is a measure of available moisture, estimated using a bucket model (Cramer and Prentice 1988). The inputs include latitude, which is used to calculate insolation potential, soil water capacity from a global 0.5° gridded dataset developed by Prentice *et al.* (1992), 'daily' temperature, precipitation, and cloudiness values estimated from the monthly means of these variables. The use of AET/PET takes into account the seasonal patterns of variation in both the supply of precipitation and the transpiration and evaporative demands. This measure is preferred to a simple measure of precipitation as it better reflects limitations of moisture supply experienced by organisms. Species' European distribution patterns have been shown more frequently to match patterns in AET/PET than patterns of seasonal precipitation (Huntley *et al.* 2007).

These variables have been successfully used to model breeding ranges in Europe and Africa (Hill *et al.* 1999; Huntley *et al.* 2007; Thomas *et al.* 2004) and are suggested to reflect the three principal limitations on growth and distribution (Huntley 1995). However, Huntley *et al.* (2007) note that although the models fitted using these variables can predict the distributions of the majority of breeding bird species in Europe

with reasonable success, this should not be taken to imply that these variables alone are affecting or having a direct influence upon the breeding distributions of European birds. One obvious example of this is migratory birds, upon which winter cold cannot have a direct influence on breeding distributions. However, this winter temperature may determine the distribution of plant species (Woodward 1987) and food availability and abundance, thereby influencing the distributions of these migratory bird species indirectly.

Modelling Approach

To be directly comparable to the models previously applied to European birds in Huntley *et al.* (2007, 2008) we used locally-weighted regression (Cleveland and Devlin 1988), which makes no *a priori* assumptions about the form of the relationship between the probability of species' occurrence in a grid cell and bioclimatic variables, to fit species-climate response surfaces (CRS) (Huntley *et al.* 2007). CRS describe the form of the relationship between the distribution of a species and the bioclimatic variables described above. Response surfaces are fitted to the species' distribution data and represent the probability of each species' occurrence for combinations of values of these three climate variables (Huntley 1995).

We fitted CRS models to each breeding bird species over the whole of Europe and North Africa to simulate the species' potential distribution. This surface was then used to evaluate the simulated species probability of occurrence. To test the performance of models including and excluding the extra-European data, we assessed model fit only for the European region, comparing simulated occurrences from both approaches to the EBCC Atlas data (Huntley *et al.* 2007).

To change the continuous suitability surfaces for a species across to Europe to presence absence data, to allow comparison with the binary recorded data, a threshold value of probability of occurrence was used. Any probabilities exceeding this threshold indicated a predicted presence and likewise probabilities lower than this threshold indicate a predicted absence. Often this threshold is set at 0.5. However, a more accurate approach has been adopted by many including Huntley *et al.* (1995 and 2004), where goodness-of-fit between the model prediction and the observed distribution of the species is maximised. An appropriate measure of goodness-of-fit must be used to determine the threshold probability and compare the predicted pattern of presence and absence, taking

each successive probability value as the potential threshold (Huntley *et al.* 2007). Goodness-of-fit measures are based upon a 'confusion matrix'. This contains information regarding actual and predicted classifications and the performance of these classification systems is evaluated using data in the matrix (Table 2.2.1).

Table 2.2.1 A confusion matrix, used to evaluate the performance of SDM data (after Kohavi and Provost, 1998). *a* – The number of correct predictions that a species is present, *b* – The number of incorrect predictions that a species is absent, *c* – The number of incorrect predictions that a species is present, *d* – The number of correct predictions that a species is absent.

Model Predictions	**Observations**	
	Present	Absent
Present	*a*	*b*
Absent	*c*	*d*

As discussed by Manel *et al.* (2001), these four values can be used as a basis to compute many different measures with their own advantages and disadvantages. To enable a direct comparison, the goodness-of-fit method used here is Cohen's Kappa '*k*' (Cohen 1960) (also used by Huntley *et al.* 2007).

Using Cohen's *k* as the goodness-of-fit measure enables a quantification of the level of agreement between simulated and actual distributions (Huntley *et al.* 2007). There are many alternate measures of goodness-of-fit (e.g. True Skill Statistic (TSS), Explained Sum of Squares (ESS), R^2). The advantages of Cohen's *k* over many of these measures is that Cohen's *k* takes into account the extent to which a model may make correct predictions by chance. This enables an assessment of how much better a model performs in comparison to a random assignment of the equivalent numbers of presences and absences (Cohen 1960).

Cohen's *k* was evaluated for all possible threshold probabilities between 0.000 and 1.000 at intervals of 0.001. The threshold probability was taken as that which gave the maximum value of *k*. This enables a measurement of the extent to which presences and absences have been correctly predicted for each grid cell across the entire grid.

Cohen's *k* has been shown to be strongly affected by the prevalence of the species being modelled (Huntley *et al.* 2004). An alternative measure which is used to attempt to overcome this sensitivity to prevalence is the calculation of the area under the curve

(AUC) for a receiver operating characteristic (ROC) (Fielding and Bell 1997) plot of sensitivity against (1- specificity) for all possible values of threshold probability (Metz 1978). Specificity is defined as the proportion of true negatives correctly predicted and sensitivity as the proportion of true positives predicted correctly to construct an ROC (Huntley *et al.* 2007). AUC is the measure generally accepted as the best way of evaluating model performance (Elith et al. 2006), providing a threshold-independent measure of model performance (Peterson 2006). Therefore the AUC values for each model have also been evaluated. The performance of goodness-of-fit measures based on kappa and AUC values have been quantified (Table 2.2). The model fitted to each breeding bird species, over the whole of Europe and North Africa, has then been used to simulate the species' potential distribution, using only the EBCC cells to ensure a direct comparison with A Climatic Atlas of European Breeding Birds.

Table 2.2.2 Interpretation of Cohen's *k* (Monserud 1990) and AUC (Swets 1988) values.

k	**Model Performance**	**AUC**	**Model Performance**
≥0.85	Excellent	>0.9	High
0.7≤ <0.85	Very Good		
0.55≤ <0.7	Good	0.7< ≤0.9	Useful
0.4≤ <0.55	Fair		
<0.4	Poor/Very Poor	0.5< ≤0.7	Low

The values of Cohen's *k* and AUC from model outputs including presence/absence data from Europe plus Turkey, Cyprus and North Africa were directly compared to the equivalent species model outputs produced by the Climatic Atlas, using only the EBCC European grid cells. A two-tailed, paired T-test with unequal variance was used to determine if any difference between the two model approaches is statistically significant.

2.2.2 Comparing Models

It is not only the data used in the model which affects the accuracy of the fit; the SDM used can also affect the precision of predictions (Hanspach *et al.* 2011).

A wide variety of SDMs are available. These models make underlying assumptions about how environmental factors control the distribution of species and communities

(Guisan and Zimmermann, 2000). Each model type has its own advantages and disadvantages, depending on the dataset being used. Van Horne (2002) suggests that there is no single 'best' modelling technique, as the choice of technique is closely related to the objective. In this analysis, I compare the climate response surface model (CRS) used in the previous section to the model fits of generalised additive models (GAM) and maximum entropy models (MaxEnt), to assess model performance. Models are compared by evaluating the relative support for each model from the observed data (Johnson and Omland 2004); in this case using measures of goodness-of-fit.

CRS, as previously discussed, is a presence-absence modelling approach. GAM is a related generic methodology, using presence/absence data. GAMs replace linear functions in GLMs with an additive function, using scatter plot smoothers to generalise the usual Fisher scoring procedure for computing maximum likelihood estimates (Hastie and Tibshirani 1986). MaxEnt is a presence-only species distribution modelling approach which maximises entropy in covariate space (Phillips *et al.* 2006). Only presence data are used, along with background data (all grid cells), to model probability of species presence. MaxEnt minimises the relative entropy between two probability densities defined in feature space Elith *et al.* (2011) and is an effective SDM technique (as it removes the problems of unreliable absence records). However, the removal of absence records can also be viewed as a potential flaw in the MaxEnt approach. Areas in which species have become extinct due to, for example, regular disturbances, may well be suitable in terms of the variables being modelled but unsuitable for other reasons. The inclusion of absences helps impose the unsuitability upon a SDM. Another advantage of presence-only models is that they can minimise problems of false-absences which result from the varying levels of species detectability. However, Elith *et al.* (2011) suggest that, when modelling using presence/absence data, modelling approaches which take into account absence should be used because they are less susceptible to problems of sample selection bias (and, hence, generally more accurate).

The most robust SDMs, which produce the best fitted data from this analysis, will be used in the next chapter to calculate CSTs and, subsequently, climatic change indicators.

Species Distribution and Bioclimatic Data

The species distribution data used was the same as in 2.2.1, i.e. EBCC plus data for North Africa, Turkey and Cyprus and included the same 496 species (Appendix 6.1). For running GAMs and CRS the species distribution data were in a presence/absence format; however, as MaxEnt is a presence only modelling approach, the dataset was transformed to only include presences and these were modelled in response to the background data (the whole grid). The bioclimatic data used was the same as that described in section 2.2.1

Model Construction and Evaluation

CRS, GAMs and MaxEnt were used to model the relationship between bioclimatic variables and the probability of species' occurrence. These SDMs are widely utilized, robust modelling approaches. CRS models were fitted using locally weighted regression (Cleveland and Devlin 1988; Huntley *et al.* 1995). GAMs were fitted using a spline smoother, binomial error distribution and a logistic function using the GAM package in the statistical package R 2.11.1 (http://www.r-project.org). MaxEnt was also fitted in R 2.11.1 using the MaxEnt package (version 3.1; http://www.cs.princeton.edu/~schapire/MaxEnt/; Phillips *et al.* 2004, 2006).

Evaluating Model Performance

Each model was fitted to the observed data and model performance was assessed using AUC and *k* values to indicate goodness-of-fit (Table 2.2). The performance of models in comparison to each other was assessed using analysis of variance (ANOVA) tests with the goodness-of-fit value as the dependent variable (both AUC and *k*). Tukey's HSD (Honestly Significant Difference) post–hoc test was used to determine if there was any significant difference between goodness-of-fit values between model techniques and, if so, which of the models performed best. Tukey's test performs multiple comparisons of means at a 95% family-wise confidence level. Tukey's HSD test compares the means of every treatment to the means of every other treatment; it applies simultaneously to all pair-wise comparisons and identifies where the difference between two means is greater than the standard error would be expected to allow (Jaccard *et al.* 1985).

2.3 Results

2.3.1 Performance of SDM Using Additional Species Presence/Absence Data

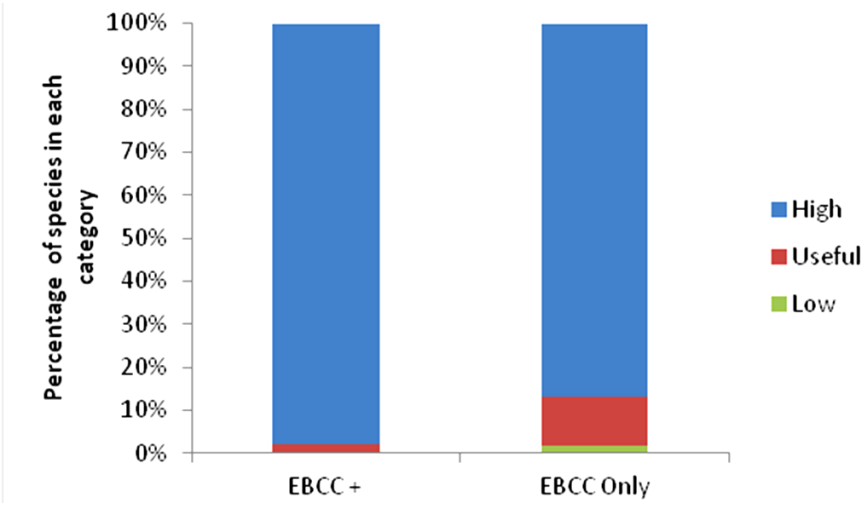
A comparison between the SDM outputs of the two sets of species distribution data: EBCC, which contained only the bird distribution data collated by the EBCC (see 2.2.1) and EBCC+ which included EBCC data along with the addition of digitised data from North Africa, Turkey and Cyprus showed that goodness-of-fit measures were significantly higher for the EBCC+ data that includes the southern and south eastern range boundaries of European breeding bird species (AUC values; $F(2, 1485)=229.2$, $p=<0.001$ *k* values; $F(2, 1485)=527.2$, $p=0.001$).

Table 2.3.1 Comparison between minimum, median and maximum values of goodness-of-fit data (Cohen's *k* and AUC), including standard deviation as a measure of variance of the performance of SDMs produced using the two sets of data. EBCC=goodness of fit data calculated using the distribution data collated by the European Breeding Bird Council (EBCC), EBCC+ refers to the outputs produced using the same EBCC data supplemented with species distribution data from North Africa, Turkey and Cyprus

	K		**AUC**	
	EBCC+	**EBCC**	**EBCC+**	**EBCC**
MIN	0.233	0.000	0.846	0.5
MAX	1.000	1.000	1.000	1.000
MEAN	0.734	0.707	0.967	0.939
STDEV	0.150	0.111	0.068	0.020

The goodness-of-fit results are more spread when using data from EBCC only (Table 2.3.1, Figure 2.3.1) as, although both groups produced the same maximum *k* and AUC scores of 1.000 and standard deviation is greater for EBCC+, the mean and minimum values from EBCC were lower than those produced by EBCC+ data. For example, the minimum AUC value produced by the larger data set (EBCC+) is still rated as 'useful' whereas the minimum value from the Climatic Atlas is at the lowest end of 'poor' (Table 2.2.2 and 2.3.1). Importantly, 100% and 94% of species model performance data from EBCC+ are in the useful-good/good-excellent categories, respectively, whereas 13% of kappa values for EBCC only data fall within the poor-fair categories (Figure 2.3.1).

A)



B)

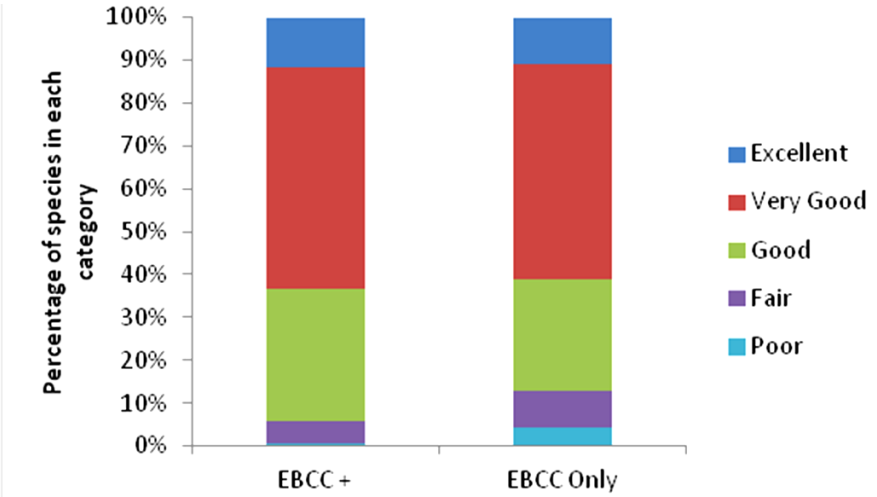


Figure 2.3.1 Comparison of goodness of fit values (A-AUC, B-Cohen's *k*) to evaluate the performance of SDMs produced using the two sets of data (EBCC+ and EBCC). Bars indicate the percentage of species in each category (Categories from Table 2.2.2).

2.3.2 Model Comparisons

The goodness-of-fit values from each modelling approach (CRS, GAM and MaxEnt) were explored to determine the most accurate of the SDM methods, using only the EBCC+ outputs (Fig. 2.3.2).

Table 2.3.2 Comparison between minimum, mean and maximum values of goodness-of-fit data (Cohen's *k* and AUC), including standard deviation as a measure of variance of the performance of SDMs produced using the three separate modelling techniques (CRS, GAM, MaxEnt).

	KAPPA			AUC		
	CRS	**GAM**	**MaxEnt**	**CRS**	**GAM**	**MaxEnt**
MIN	0.399	0.106	0.002	0.850	0.495	0.018
MAX	1.000	1.000	0.963	1.000	1.000	0.999
MEAN	0.776	0.623	0.550	0.982	0.950	0.741
STDEV	0.118	0.189	0.191	0.019	0.049	0.213

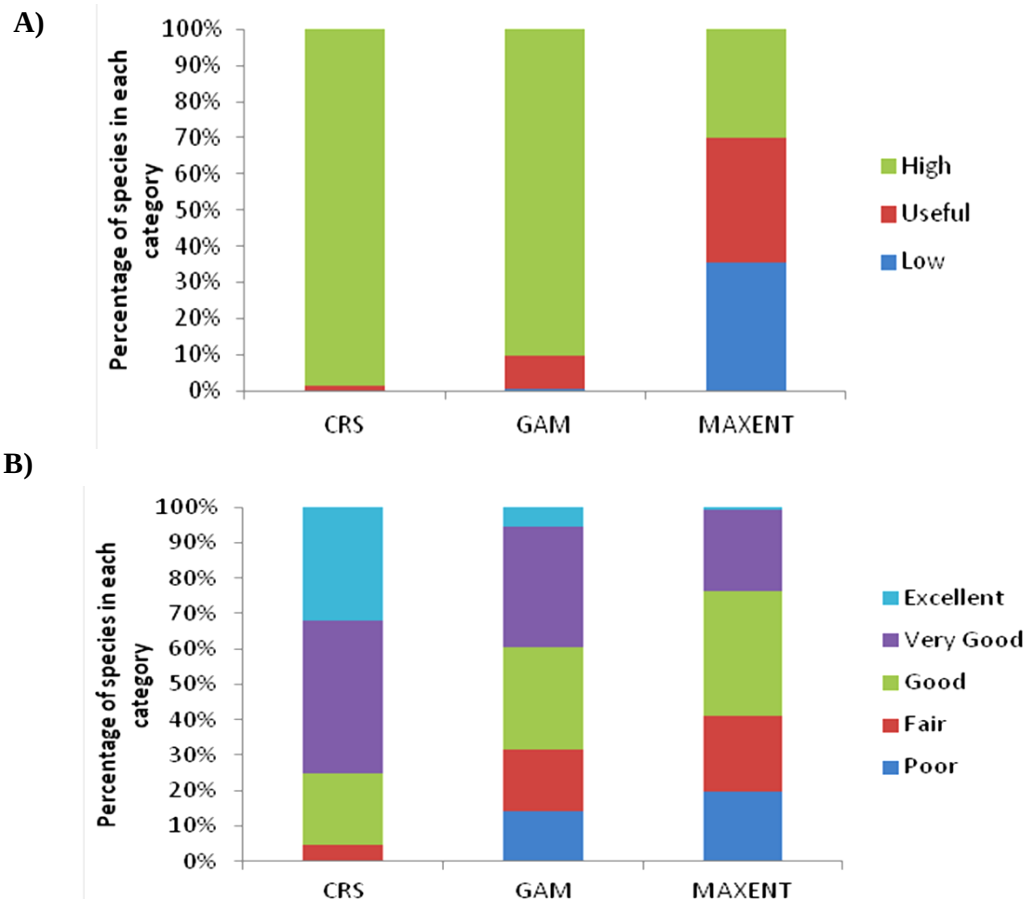


Figure 2.3.2 Further examination of the spread of goodness-of-fit data (A-AUC and B-Cohen's *k*) between the three modelling techniques (CRS, GAM and MaxEnt).

Goodness-of-fit from the three modelling methods were significantly different (ANOVA: Cohen's *k* n=497 F=229.2, p<0.001; AUC n=497 F=527.2, p<0.001). Specifically, CRS and GAM goodness of fit were both significantly better than MaxEnt (Tukey's HSD: Cohen's *k* p<0.001 and p<0.001 respectively, AUC p<0.001 and p<0.001 respectively) and CRS goodness of fit was significantly better than that of the GAM (Tukey's HSD: Cohen's *k* p<0.001, AUC p<0.001). Taken together, these results suggest that CRS is the model which fits this data best, closely followed by GAM, with MaxEnt performing worst.

2.4 Discussion

Current and predicted levels of climatic change portray unprecedented challenges for the management of biological conservation (Stern 2007). Therefore policy makers are looking increasingly to modelled projections of species' distributions under future climates to inform conservation policy, invasive species management and disease control measures (Beale and Lennon 2012). Given the potential of SDMs to influence policy and management we must insure that the information and data used to formulate such projections is the best available, and is as full and accurate as possible (Sinclair *et al.* 2010). This study used SDMs to simulate species distribution predictions under imposed climatic scenarios. Predictions were compared to observed species distribution patterns, thereby enabling a validation of the application of SDMs to provide valuable information on projections of future species' distributions. The major findings were that the inclusion of an increased amount of species' distribution data improved SDM simulations of species' distributions, and that of the three SDMs tested CRS and GAM both significantly outperformed MaxEnt.

The purpose of this chapter was to test and validate the models and data to be used in the main focus of this work, producing an indicator of the impacts of climatic change on levels of biodiversity. It is widely acknowledged that significant levels of variability exist with the projections of SDMs and that assessment of model performance is crucial (Mouton *et al.* 2010). Thorough testing reduces the uncertainty of outputs and improves accuracy through the selection of the most consensual projections (Araujo *et al.* 2005).

The greatest differences between the recorded climatic atlas goodness-of-fit values and those calculated using the additional data were, unsurprisingly, for those species with

restricted European distributions that have a substantial proportion of their breeding range in Turkey and Cyprus, such as *Serinus pusillus, Tetraogallus caspius, Francolinus francolinus, Puffin assimilis, Tetrao mlokosiewiczi* and *Psittacula krameri.* Therefore, the inclusion of these data would be expected to improve goodness-of-fit measures if the fit within Turkey and Cyprus was included in this calculation. However, as only the cells within the EBCC dataset used by the Climatic Atlas were included to test fitting, this provides strong evidence that including these grid cells, and their related bioclimatic variable suitable for the species in question, provides a more accurate simulation of the extent of the distribution of these species throughout Europe.

Despite the inherent limitations of SDMs (Araujo *et al.* 2005; Araujo and Guisan 2006; Diniz-Filho *et al.* 2009), they have enabled significant progress in the climatic change debate; SDMs have promoted ecological theory and biodiversity conservation into the non-scientific arena. They have provided clear and concise warnings, allowing biodiversity issues to permeate broader discussions of climatic change (Sinclair *et al.* 2010). SDM techniques are acknowledged to differ in their modelling performance and measures of predictive accuracy are needed to test the precision of these methods and reduce the uncertainty of predictions (Araujo *et al.* 2005; Marmion *et al.* 2009). Choice of method should always be contingent on the goals and kinds of distributions being modelled (Segurado and Araujo 2004). Both measures of goodness-of-fit demonstrate that model performance is improved by the addition of data covering the southern and SE range boundaries of European breeding bird species. This suggests that models including more presence/absence data outperform models produced by the Climatic Atlas using only EBCC species distribution data. It was logical, therefore, to utilise the models that incorporated the North African and SE European range margins to develop CST in subsequent chapters. This significantly increases the accuracy of species distribution forecasts, and thus provides a more valuable application for different conservation biological and biogeographical issues (Marmion *et al.* 2009) (in this case the production of biodiversity indicators of climatic change).

CRSs and GAMs provided the most accurate SDM fits. In order to ensure the reliability and usefulness of the indicators produced, only these two SDM techniques will be used to calculate CSTs to generate climatic change indicators. MaxEnt was poor at estimating those species which have low prevalence, probably partly as it does not take prevalence into account and does not penalise heavily for over-prediction. Elith *et al.*

(2011) suggest that MaxEnt struggles to predict species distributions using a sample size of less than 15 presence only data points. However, with such a large area of bioclimatic data being used, these results would suggest that MaxEnt struggles to predict species distributions accurately for those species with sample sizes far above the 15 data point cut off, if those species have a restricted or discontinuous breeding distribution (e.g. *Parus cyanus*, *Emberiza leucocephalos*, *Sitta whiteheadi*, *Tetrao caspius*, *Falco biarmicus*, *Streptopelia senegalensis*, *Larus ichthyaetus*, *Gelochelidon nilotica*, *Xenus cinereus*). Furthermore, when modelling species distributions from occurrence records, as is carried out by MaxEnt, additional data is required to represent the range of environmental conditions in the modelled region. These background data are drawn at random from the entire region, whereas occurrence collection can often be spatially biased toward easily accessed areas. Therefore, since the spatial bias generally results in environmental bias, the difference between occurrence collection and background sampling may lead to inaccurate portrayal of species distribution (Phillips *et al.* 2009). Furthermore, the CRS model could be over-fitting, as we only tested models on the full dataset, and not on independent test data.

As the data used are sourced from formal biological survey with large amounts of quantified data on species presence/absence, then it is logical to utilise modelling approaches that take advantage of both presence and absence data, and it is not unexpected that such models prove better fits to the observed data. This does not suggest, however, that presence-only techniques are not vital to investigate genuine presence-only datasets (Elith *et al.* 2011). Reliability is a fundamental consideration when producing indicators. The more reliable an indicator, the more accurately it is able to represent and communicate biological processes and therefore the more useful it will prove to be to inform policy makers (Gregory *et al.* 2005; Carey 2009).

This work has demonstrated the importance of using complete data sets when calculating species distributions. The inclusion of the southern and south eastern edges of European breeding bird ranges increased the goodness-of-fit of SDM predictions/simulations. Although Araujo *et al.* (2005) argue that perfect validation of models may not be conceptually possible, it is important to ensure as far as possible when producing an indicator of climatic change, that the species distribution data used is as full and as accurate as possible to ensure the construction of a reliable indicator. This exploration of SDMs has also demonstrated that GAM and CRS models tested

performed best with the type of dataset that will be used to generate predictions of species distributions for constructing climatic change indicators.

Further, more time-consuming, work to validate the findings presented here could include a k-fold validation. This is also often referred to as the 'leave one out approach' which, as the name suggests, involves randomly splitting the dataset into mutually exclusive subsets of approximately equal sizes and repeatedly fitting the model, each time using all but one of the data items as an input (Kohavi 1995). This would help to minimise the effect of spatial autocorrelation within the dataset. Doswald *et al.* (2009) compared two modelling techniques (GAM and CRS) looking at both the fit of the full dataset and the results after k-fold partitioning and found variation in the model that performed best when using this approach. The results from this analysis demonstrate a more significant difference between modelling techniques than those investigated by Doswald *et al.* (2009) but the fact remains that the undertaking of k-fold partitioning would provide a more accurate assessment of these models. A similar 'leave a block out' approach was used in the Climatic Atlas to validate the model outputs; therefore, including this method would ensure these results were more directly comparable. It would also further improve the validity of the comparisons between models (Section 2.3); however, such a solution is more difficult to implement on more complex estimation algorithms (i.e. GAMs; Guisan and Zimmermann 2000). Furthermore, Gonzalez *et al.* (2010) suggest that AUC values can be misleading when assessing the predictive ability of a model; they champion the use of omission curves in addition to AUC values to assess model performance.

An interesting extension to this exploratory work would be the use of this data to simulate species' potential future breeding distributions, to compare the impact of using models including more southern range edge data to the simulated potential late 21st century distributions by Huntley *et al.* 2007, in order to further understand how ecological systems may behave in future, changed conditions (Araujo *et al.* 2005; Evans *et al.* 2012).

By including extra data into SDM calculations and comparing this to previous predictions carried out using the same SDM method it has been shown that increasing knowledge of species' distribution significantly improves predictions of distribution. Using the same increased population data to compare the performance of three different

SDMs (GAM, CRS and MaxEnt) showed that CRS predicted species distributions most accurately and that CRS and GAM both significantly outperformed MaxEnt.

2.5 References

Araujo, M.B., Pearson, R.G., Thuiller, W. and Erhard, M. (2005) Validation of species-climate impact modles under climate change. *Global Change Biology* **11** 1504-1513

Araujo, M.B., Whittaker, R.J., Ladle, R.J. and Erhard, M. (2005) Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography* **14** 529-538

Araujo, M.B. and Guisan, A. (2006) Five (or so) challenges for species distribution modeling. *Journal of Biogeography* **33** 1677-1688

Araujo, M.B., Alagador, D., Cabeza, M., Nogues-Bravo, D. and Thuiller, W. (2011) Climate change threatens European conservation areas. *Ecology letters* **14** 484-492

Arguez, A. and Vose, R. (2011) The definition of the standard WMO climate normal: the key to deriving alternative climate normals. *Bulletin of the American Meteorological Society* **92** 699–704

Beale, C.M. and Lennon, J.J. (2012) Incorporating uncertainty in predictive species distribution modelling. *Philosophical Transactions of the Royal Society: Biological Sciences* **367** 247-258

Both, C. and Visser, M.E. (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411** 296-298

Carey, C. (2009) The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the* Royal *Society B: Biological Sciences* **364** 3321-3330

Cleveland, W.S. and Devlin, S.J. (1988) Locally weighted regression: an approach to regression analysis by local fitting. *Journal of American Statistical Association* **83** 596-610

Cohen, J. (1960) A coefficient of agreement for nominal scales. *Educational and Physiological Measurements*, **20** 37-46

Crammer, W. and Prentice, I.C. (1988) Simulation of soil moisture deficits on a European scale. *Ibis* **142** 150-151

Diniz-Filho, J.A.F., Bini, L.M., Rangel, T.F., Loyola, R.D., Hof, C., Nogués-Bravo, D. and Araújo, M.B. (2009) Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. *Ecography* **32** 897-906

Doswald, N., Willis, S.G., Collingham, Y.C., Pain, D.J., Green, R.E. and Huntley, B. (2009) Potential impacts of climate change on the breeding and non-breeding ranges and migration distance of European *Sylvia* warblers. *Journal of Biogeography* **36** 1194–1208

Elith, J. Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira. R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S. and Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29** 129-151

Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E. and Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* **17** 43-57

Evans, M.R., Norris, K.J. and Benton, T.G. (2012) Predictive ecology: systems approaches. *Philosophical Transactions of the Royal Society: Biological Sciences* **367** 163-169

Fielding, A. H. and Bell, J. F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24** 38-49

Gonzalez, S.C., Soto-Centeno, J.A. and Reed, D.L. (2011) Population distribution models: species distributions are better modelled using biologically relevant data partitions. *BMC Ecology* **11:20**

Guisan, A. and Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling* **135** 147–186

Franklin, J. (2009) *Mapping species distributions: spatial inference and prediction.* Cambridge University Press, Cambridge

Gregory, R.D., van Strien, A.J., Vorisek, P., Gmelig Meyling, A.W., Noble, D.G., Foppen R.P.B. and Gibbons, D.W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B* **360** 269-288

Gregory, R.D., Willis, S.G., Jiguet, F., Voříšek, P., Klvaňová, A., van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D. and Green, R.E. (2009) An indicator of the impact of climatic change on European bird populations. PLoS ONE 4 e4678

Grinnell, J. (1917) The niche-relationships of the California thrasher. *The Auk* **34** 427-433

Guisan, A. and Zimmerman, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135** 147-186

Guisan A. and Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8** 993-1009

Hagemeijer, E.J.M. and Blair, M.J. (eds.) (1997) *The EBCC atlas of European breeding birds: their distribution and abundance*. 903 T. and A.D. Poyser, London

Hanspach, J., Kuhn, I., Schweiger, O., Pompe, S. and Klotz, S. (2011) Geographical patterns in prediction errors of species distribution models. *Global Ecology and Biogeography* research paper.

Hastie, T. and Tibshirani, R. (1986) Generalized additive models. *Statistical Science* **1:3** 297-318

Hill, J.K., Thomas, C.D. and Huntley, B. (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London* **266** 1197-206

Hirzel, A. and Guisan, A. (2002) Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling* **157** 331–341

Hitch, A.T. and Leberg, P.L. (2007) Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology* **21** 534-539

Hole, D., Willis, S.G., Pain, D.J, Fishpool, L.D., Butchart, S.H.M., Collingham, Y.C., Rahbek, C. and Huntley, B. (2009) Projected impacts of climate change on a continentwide protected area network. *Ecology Letters* **12** 420–431

Huntley, B. (1995) Plant species' response to climate change: implications for the conservation of European birds. *Ibis* **137** 127-38

Huntley, B., Green, R.E., Collingham, Y.C., Hill, J.K., Willis, S.G., Bartlein P.J., Cramer, W., Hagemeijer W.J.M and Thomas, C.J. (2004) The performance of models relating species geographical distributions to climate is independent of trophic level. *Ecology Letters* **7** 417–426

Huntley, B., Green, R. E., Collingham, Y. and Willis, S. G. (2007). *A climatic atlas of European breeding birds*. Durham, Sandy and Barcelona: Durham University, RSPB and Lynx Editions

Hutchinson, G.E. (1957) "Concluding remarks". *Cold Spring Harbor symposia on quantitative biology* **22** 415–427

Jaccard, J., Becker, M.A. and Wood, G. (1984) Pairwise multiple comparison procedures: A review. *Psychological Bulletin* **96** 589-596

Johnson, J.B. and Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution* **19** 101–108

Kohavi, R. (1995) A study of cross-validation and bootstrap for accuracy estimation and model selection. *International Joint Conference on Artificial Intelligence* 7

Kohavi, R. and Provost, F. (1998) "Glossary of terms." In: *Editorial for the special issue on applications of machine learning and the knowledge discovery process, machine learning* **30**

Mac Nally, R. (2002) Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodiversity and Conservation* **11** 1397–1401

Mannel, S., Williams, H.C. and Ormerod, S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* **38** 921-31

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., and Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions* **15** 59-69

Metz, C.E. (1978) Basic principles of ROC analysis. *Seminars in nuclear medicine* **4** 283-98

Monserud, R.A. (1990) *Methods for comparing global vegetation maps*, No. WP-90-40. International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria

Mouton, A.M., De Baets, B. and Goethals, P.L.M. (2010) Ecological relevance of performance criteria for species distribution models. *Ecological Modelling* **221**1995-2002

Müller, M.J. (1982) *Selected climatic data for a global set of standard stations for vegetation science.* 306 Dr. W. Junk Publishers, The Hague

New, M., Hulme, M. and Jones, P. (1999) Representing twentieth-century space-time climate variability. Part I: Development of a 1961-90 mean monthly terrestrial climatology. *Journal of Climate* **12** 829-56

Peterson, A.T. (2006) Uses and requirements of ecological niche models and related distributional models. *Biodiversity Informatics* **3** 59-72

Phillips, S. J., Dudik, M. and Schapire, R.E. (2004) *A maximum entropy approach to species distribution modelling*. 655-662 IN Proceedings of the 21st International Conference on Machine Learning. ACM Press, New York

Phillips, S. J., Anderson, R.P. and Schapire, R.E. (2006) Maximum entropy modelling of species geographic distributions. *Ecological Modelling* **190** 231-259

Phillips, S.J., Dudík, M., Elith, J., Graham,C.H., Lehmann, A., Leathwick, J. and Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* **19** 181–197

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. and Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography* **19** 117-34

Roselarr, C.S. (2000) *Songbirds of turkey: taxonomy, morphology, distribution: an atlas of biodiversity of Turkish passerine birds* Pica Press 240

Sakamoto, C.M., Gifford, R.O. and Koh, Y.O. (1977) Growing degree-days in Nevada. *Agricultural Experiment Station* College of Agriculture, University of Nevada-Reno, and U.S. Department of Commerce

Segurado, P and Araujo, M.B. (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography* **31** 1555-1568

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology and Evolution* **19** 605–611

Sinclair, S.J., White, M.D. and Newell, G.R. (2010) How useful are species distribution models for managing biodiversity under future climates? *Ecology and Society* **15** 1-13

Snow, D. W. and Perrins, C. M. (1998). *The birds of the western palearcti.c* Concise Edition. Oxford University Press, Oxford 1832

Stern, N. (2007) *Stern review: the economics of climate change*. Cambridge University Press, Cambridge

Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science* **240** 1285-1293

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqeira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. and Williams, S.E. (2004) Extinction risk from climate change. *Nature* **427** 145-8

Thomas, C.D. and Lennon, J.J. (1999) Birds extend their ranges northwards. *Nature* **399** 213

Torti, V.M. and Dunn, P.O. (2005) Variable effects of climate change on six species of North American birds. *Oecologia* **145** 486-495

Van Horne, B. (2002) *Approaches to habitat modelling: the tensions between pattern and process and between specificity and generality*. In: Predicting species occurrences: issues of accuracy and scale (eds Scott, J.M., Heglund, P.J., Morrison, M.L., Raphael, M.G., Wall, W.A., and Samson, F.B.). Island Press, Covelo, California

Wiens, J.A. (2002). *Predicting species occurrences: progress, problems, and prospects. In: Predicting species occurrences: issues of accuracy and scale* (eds Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A. and Samson, F.B.). Island Press, Covelo, California 739–749

Williams, P.H. (1986) *Environmental change and the distributions of British bumble bees (Bombus latr.)*. Department of Entomology, British Museum (Natural History) 50-61

Woodward, F.I. (1987) *Climate and plant distribution*. Cambridge University Press, Cambridge

Chapter 3- The Relationship Between Trends in Climatic Suitability and Bird Population Trends Across Europe

3.1 Introduction

Climatic change is widely cited as one of the most powerful pressures currently impacting upon natural processes. Much evidence suggests that bird population trends are already responding to these changes (Both and Visser 2001, Torti and Dunn 2005, Hickling *et al.* 2006, Hitch and Leberg 2007, Carey 2009) and that these trends will continue to alter in response to future climatic warming (Thomas *et al.* 2004, Green *et al.* 2008, Gregory *et al.* 2009, Renwick *et al.* 2012). The process of monitoring population trends and changes is vital given the magnitude of climatic change. Monitoring facilitates the auditing of past management decisions and informs future choices (Jones 2011). Species trend data enable monitoring of both small and large scale changes in populations. There are many sources from which such data can be obtained. One such source of trend data is the high level summary reports of population trend statistics (e.g. IUCN red list 2002). However, such reports tend to focus specifically upon threatened and well-studied species and can overlook common taxa. These summaries, therefore, do not necessarily provide a good measure of the changes in nature, and the rates at which changes, such as loss of biodiversity, occur (Gregory *et al.* 2005). Population trends published in previous literature provide another source of species data (e.g. Osborne *et al.* 2001). Such compiled population trend data has benefits in comparison to data extracted from high level summaries regarding species trends, as it can be updated more regularly (Gregory *et al.* 2005).

A further method of generating summary statistics on species' population trends is to extract the data from large scale monitoring programmes. This method enables the control, and therefore reduction, of selection bias (Gregory *et al.* 2005), but can under-represent those taxa which are more difficult to monitor. Bird population trends are easily accessible, as censuses of population trends throughout Europe are widespread and ongoing and involve the collection and analysis of large amounts of population data. Such censuses are undertaken by a number of different organisations in Europe: Birdlife International, the European Bird Census Council (EBCC), the Rare Breeding Birds Panel and the British Trust for Ornithology (BTO) and the Predatory Bird Monitoring Scheme.

For analyses in this chapter, I utilise bird population trend data from the Pan European Common Bird Monitoring Scheme (PECBMS). PECBMS was established in 2002 with the aim of delivering data for use in both policy and research, using population trends of common European breeding birds as bio-indicators of the general state of the wider environment, and was a collaboration between BirdLife International and EBCC. These data are collected by national monitoring schemes, using standardised methodologies and carried out by volunteers.

SDMs link species' occurrence to climate data to determine the role of climate in species' distributions (Thomas *et al.* 2004). The use of different SDMs was investigated in the previous chapter to further understanding of their predictive ability of species' responses to climatic change (see Chapter 2). Generalised Additive models (GAM) and Climate Response Surface models (CRS) have been demonstrated, through validation processes, to be viable methods for predicting species' distributions (section 2.4).

In this chapter, I assess the relationship between simulated climatic suitability for European breeding birds, produced using species distribution models (SDM), and recorded population trends. If a reliable relationship exists, projected trends could be used to estimate future population changes and to inform and influence policy and management of biodiversity (Caro and O'Doherty 1999, Julliard *et al.* 2003, Gregory *et al.* 2005, Gregory *et al.* 2007).

Previous studies have suggested that bird populations may respond to climatic change at a pan-European scale (Green *et al.* 2008, Gregory *et al.* 2009), and although these studies demonstrate that significant relationships exist between species' trend data and predicted future climatic suitability, the relationship between recent trends in bird populations and recent climatic change are weaker. Climatic change has varied spatially across Europe in recent decades, in turn, populations of species have experienced differing degrees of change. Therefore, we would expect trends to vary for a single species across the region (Behrens *et al.* 2010). Furthermore, many policy processes operate at national scales and so it is vital to understand the impact of climatic change at this scale to inform policy responses more accurately. In this study, both population trend data and the calculations of climate suitability were examined at the scale of individual countries, rather than across the entire European sub-continent.

Climatic change has already been demonstrated to be having an impact upon European breeding bird populations (McCarty *et al.* 2001, Julliard *et al.* 2003, Sekercioglu *et al.*

2008, Gregory *et al.* 2009). Based on these previous studies, species are expected to respond to the changing climate by increasing or decreasing density within their existing range, by contracting or expanding the extent of their range, or by a combination of both these factors. Therefore, I expect to find a positive correlation between simulated Climate Suitability Trend (CST) (the mean probability of species' occurrence) and the PECBMS trend. However, species' trend data may be impacted upon by variables other than climate. There is evidence to suggest that population trends of European birds vary according to biological traits such as migratory status, life history and habitat preference (Gregory *et al*. 2009). Such biological traits are potentially confounding variables which have been demonstrated to impact upon species' responses to climatic change (Thomas *et al.* 2004, Arújo and Luoto 2007, Foden *et al.* 2008).

This chapter explores the relationship between climate and the population trends provided by the PECBMS, in several ways. Firstly, the relationship between climate suitability and the PECBMS trend data for individual species is examined for each European country. Secondly, the impacts of country-level monitoring information are explored to determine whether variables such as country size and monitoring duration affect the relationship between climate and species' trend responses. Finally, the effects of species' biological traits are investigated to assess the influence of these variables upon the strength of the relationship between CSTs and population trends.

3.2 Methods

Selection of Bird Species

Trends of 145 common bird species (Appendix Table 6.1), for which European trends were available from the PECBMS were initially included in this trend data analysis. These data are derived from annual breeding bird monitoring schemes in 20 European countries (PECBMS: http://www.ebcc.info/pecbm.html) (Table 3.2.1).

Selection of Countries

Table 3.2.1 A list of countries for which the PECBMS trend data is available, including size of country and the number of years covered by the data. **Bold** = those countries for which CST was calculated.

Country	**Code**	**Size** (Number of 50km^2 cells occupied)	**Mean Number of Data Collection Years**
Austria	AT	57	11
Belgium	**BE**	**14**	**19**
Czech Republic	**CZ**	**25**	**27**
Denmark	**DK**	**51**	**33**
Estonia	**EE**	**30**	**20**
Finland	**FI**	**181**	**27**
France	**FR**	**229**	**18**
Germany	**DE**	**119**	**18**
Hungary	HU	25	10
Italy	IT	162	9
Latvia	LV	44	4
Netherlands	**NL**	**22**	**25**
Norway	NO	189	13
Poland	PL	137	9
Republic of Ireland	IE	42	11
Spain	ES	236	11
Sweden	**SE**	**169**	**34**
Switzerland	**CH**	**35**	**10**
United Kingdom	**UK**	**137**	**43**

From this initial dataset I excluded trend data for any species in a country that had <18 years of monitoring (128 species in 11 countries) (Table 3.2.1 and Appendix Table 6.1). Species with a PECBMS trend length of ≥18 years provided a compromise between quantity (number of species and countries included in the analysis) and quality (length of trend period). This approach was adopted to remove any species' trends which were considered unreliable or unrepresentative of a long term climate driven trend. This choice of length of trend data used is similar to that applied by Gregory *et al.* (2009),

who excluded all species whose trend data were only available after 1990 (with data running until 2008).

Bioclimatic Data

The bioclimatic variables used were the same as discussed previously (see Section 2.2.1): annual temperature sum above 5°C (GDD5), mean temperature of coldest month (MTCO), and an estimate of the annual ratio of actual to potential evapotranspiration (AET/PET). These variables have been demonstrated to influence species' ranges and are related to the distribution, directly or indirectly, of many Palaeartic species (Hill *et al*. 1999; Huntley *et al*. 2007). These data were taken from data provided by CRU TS 3.1 (badc.nerc.ac.uk). The CRU TS dataset consists of monthly climate observation values that are gridded at a global level at 0.5° longitude x latitude. The values for each of the three bioclimatic variables (GDD5, MTCO and AET/PET) from 1960-2008 were interpolated to the same spatial grid as the presence/absence data used in this study.

Species Distribution Data

The species distribution data were the same as those used in the previous chapter (see Section 2.2.1). These included species presence/absence data from EBCC, supplemented with data from North Africa, Turkey and Cyprus. However, only the 128 species covered by the PECBMS trend data were included (Appendix Table 6.1).

Calculating Climate Suitability

Each grid cell was assigned to the country which the largest part of the cell resided in, using the intersect function in Arc-GIS. Climate Suitability Trend (CST) was calculated by fitting Climate Response Surface (CRS) models and Generalised Additive Models (GAMs) for each species' distribution data to the climatic normal (the mean of the three bioclimatic values between 1961-1990 for any cell) (Arguez and Vose 2011). Annual values of the three bioclimatic variables were applied to the CRS and GAM SDMs to calculate the probability of occurrence, in each $50km^2$ cell, of each species in each year for which data were available between 1960–2008 (Appendix Table 6.1 shows the number of years covered by trend data for each bird species) in individual countries. These probabilities of occurrence for each year were then averaged across all squares in

each country to obtain the annual mean probability of occurrence. Ordinary least-squares linear regression was used to calculate the slope of the regression for each country between logit annual mean probability of occurrence and year (Green *et al.* 2008). The slope produced is the species' CST (referred to as GAMCST and CRSCST for the CST produced by each modelling technique).

3.2.1 CST v PECBMS Trends for European Countries

The calculation of CST makes it directly comparable to the PECBMS trend data. For each country, PECBMS values for all species were correlated with their corresponding CST values; Pearson's r (a descriptor of the degree of linear association between the PECBMS and CST) was used to determine the strength of the correlation. Both CRSCST and GAMCST were analysed in this way.

3.2.2 CST v PECBMS Relationship for Individual Species

The relationship between CST and the PECBMS trend data for each species was analysed in a similar manner to the assessment of the relationship between countries. Here, CST values for a species, in each country where the species is simulated as present, were correlated with the corresponding PECBMS trend values. This was repeated for the 109 species which were present in three or more countries. Again, Pearson's r was used to assess the strength of the correlation.

3.2.3 Impact of Country Level Monitoring Traits

Monitoring variables (duration of monitoring and country size) were assessed to determine their impact upon the relationship (Pearson's r) between PECBMS and CST. Duration of monitoring refers to the number of years of trend data available. The number of $50km^2$ cells within a country was used as a proxy for country size. These data were readily available from the PECBMS and were extrapolated from data used in previous calculations. Their impacts on the strength of the correlation between PECBMS and CST were explored and analysed using Pearson's r.

3.2.4 Impact of Species Biological Traits

Evidence from previous studies suggests that population trends of European birds vary according to breeding habitat (Gregory *et al.* 2007), migratory status (Sanderson *et al.* 2006, Both *et al.* 2010) and life history characteristics (Green 2008, Gregory *et al.*

2009). These traits were investigated to determine the possible effects of any of them on the relationship between CST and the PECBMS.

The biological traits (Table 3.2.1) considered were:

Breeding Habitat: Each of the 145 breeding bird species were allocated to one of three broad habitat types (woodland, farmland or other) according to their predominant habitat use (i.e. if more than 50% of the population in the countries contributing data to the PECBMS is judged to use one particular habitat during the breeding season). These data on habitat use were obtained from EBCC (www.ebcc.info/index.php?ID=471#Box species selection and classification).

Migratory Category: Each species was allocated to one of three migratory categories (resident, short-distance migrant or long-distance migrant)**.** This allocation was based upon information regarding the predominant migratory behaviour of breeding bird populations from Snow and Perrins (1998). *Resident*- most individuals are non migratory; *Short-distance Migrant*- populations contain substantial migratory and non-migratory elements, migratory populations make regular movements but these take place within the area covered by the PECBMS population monitoring network; *Long-distance Migrant*- all or most individuals make regular seasonal movements between the breeding range and a non-breeding range that lies outside the countries contributing data to the PECBMS.

Life History: The natural logarithm of mean body mass was used as a proxy for life history strategy as body mass has been demonstrated to be correlated with many life history variables (Green *et al.* 2008).These data were obtained from the PECBMS (http://www.ebcc.info/pecbm.html).

To determine whether the relationship between the PECBMS trend data and CST was significant when taking into account each of these traits, generalised linear mixed effects models (GLMM) were fitted to analyse the predictive value of both CRSCST and GAMCST.

GLMMs provide a flexible approach to analyse non-normal data involving random effects by combining the properties of linear mixed models (which handle random effects) and generalised linear models (which incorporate nonnormal data) to fit

parameters by maximum likelihood (Bolker *et al.* 2009). In order to make a statement generalised to an entire country/region's bird population, from a study of a fixed sample of bird species, the bird species being considered cannot be treated as fixed effect. Basic statistical methods rely on normally distributed data, however in this analysis GLMMs were used to quantify the effect of each of the predictors variables as the data are a mixture of fixed (i.e. habitat preference, migratory status) and random (i.e. CRSCST) effects. Therefore an ANOVA would be an unsuitable method of analysis, as with a categorical response variable, this would lead to invalid results. The aim here is to identify the variation among these mixed effects rather than quantify the exact effect of each predictor variable.

Population trend (PECMBS) was the dependant variable. CRSCST and GAMCST were considered to be random effect factors as these data provide a random sample of bird species data which are generalised to national and regional populations. The biological traits; breeding habitat (HAB), migratory status (MIG) and log body mass (LMS) were considered to be fixed effect factors as data are obtained from all levels of the factor which are of interest.

Akaike's Information Criterion (AIC) was used to select among fitted models, a process which trades off model fit and generality. AIC is a measure of the relative goodness of fit of a statistical model. AIC does not test how well the parameters fit the data in an absolute sense but provides a comparison between fitted models; it takes into account the number of parameters in the model and promotes parsimony (Burnham and Anderson 2002). AIC values are calculated for each model, as follows (Equation 3.2.1). Here, k is the number of parameters included in the statistical model and L is the maximised value of the likelihood function (the likelihood of observing the data given the model) for the estimated model (Burnham and Anderson 2002).

$$\mathrm{AIC} = 2k - 2\ln(L) \quad \textbf{Equation 3.2.1}$$

The preferred model is the one with the lowest AIC value; this represents the best approximation of the true model i.e. the model with the smallest expected loss of information. AIC is calculated on a relative scale, therefore it is critical to compute, and present, the AIC differences (ΔAIC) rather than actual AIC values (Buckley and Cunningham, 2002; Burnham and Anderson, 2003). ΔAIC is calculated as [AIC – min AIC], where min AIC is the smallest AIC value among all candidate models. Burnham

and Anderson (2002) suggest that values of ΔAIC between 0-2 provide substantial evidence in favour of the model, values 4-7 provide less support for the model and any model with values above 10 provide no support. There is still much debate regarding the point at which a model can be considered un-informative. Although values between 0-2 are essentially considered as good as the best model, it is also recognised that models with ΔAIC up to 6 should not be discounted (Richards 2005, Richards *et al.* 2011). Therefore, in this work, models with ΔAIC ≤ 6 were considered. The Akaike weight for a model is the relative likelihood of the model divided by the sum of likelihood values across all models.

The model likelihood of these traits was analysed using R 2.11.1 (http://www.r-project.org). The GLM function was used in the MuMin package: multi-model inference (Barton 2009), this package contains functions for model selection and model averaging based on information criteria (AIC). GLM was run to enable model selection and calculate AIC (R Development Core Team, 2006). Models were run for all combinations of traits, including CST as well as the potentially confounding traits: breeding habitat, migratory strategy and body mass.

3.3 Results

3.3.1 CST v PECBMS Trends for European Countries

Five of the 11 countries included in this analysis showed a significant positive association between the PECBMS trend and CST (Table 3.3.1, Figure 3.3.1).

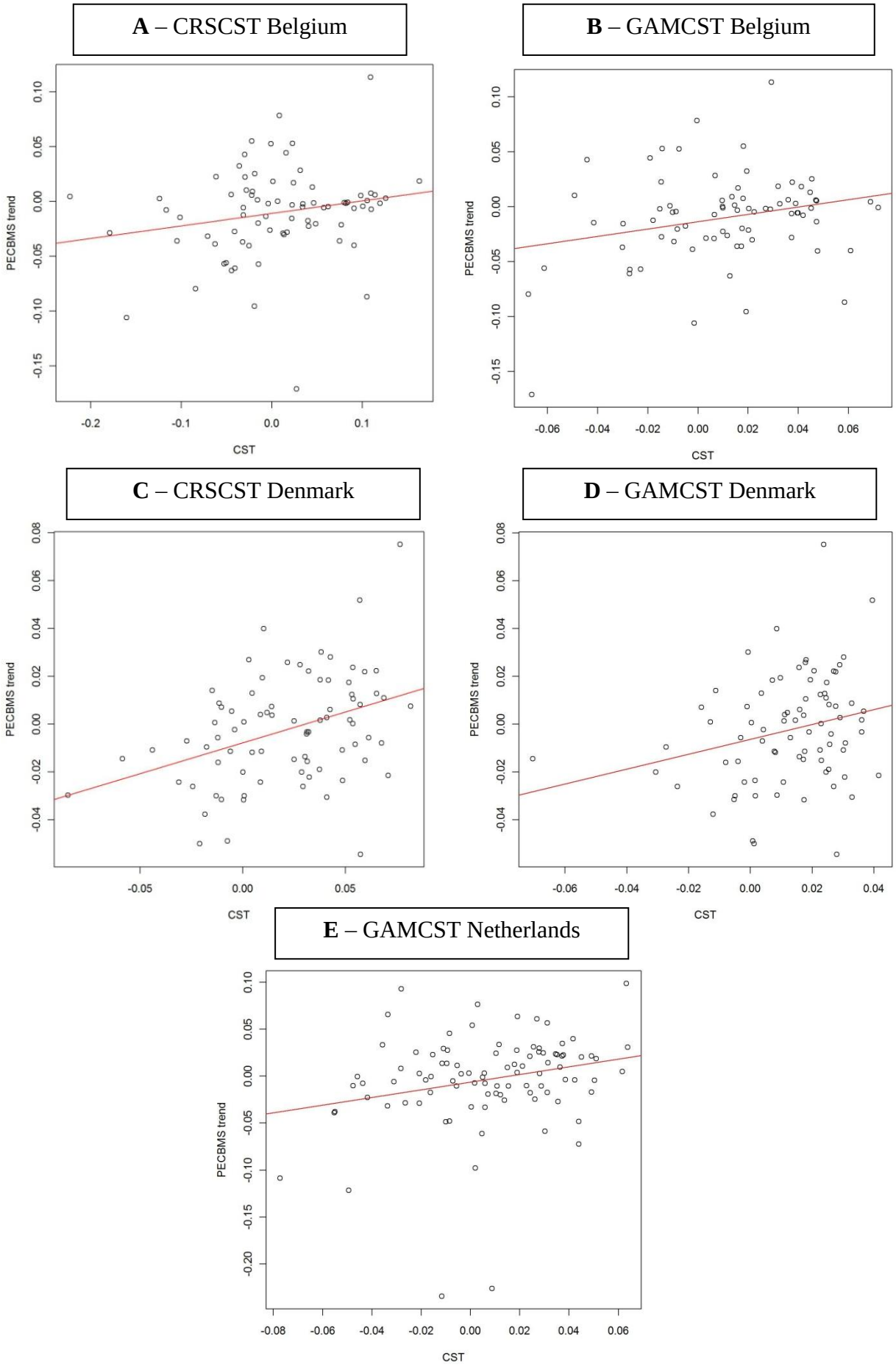


Figure 3.3.1 The association between CST (CRS and GAM) and PECBMS trend for each country in which the association was significant.

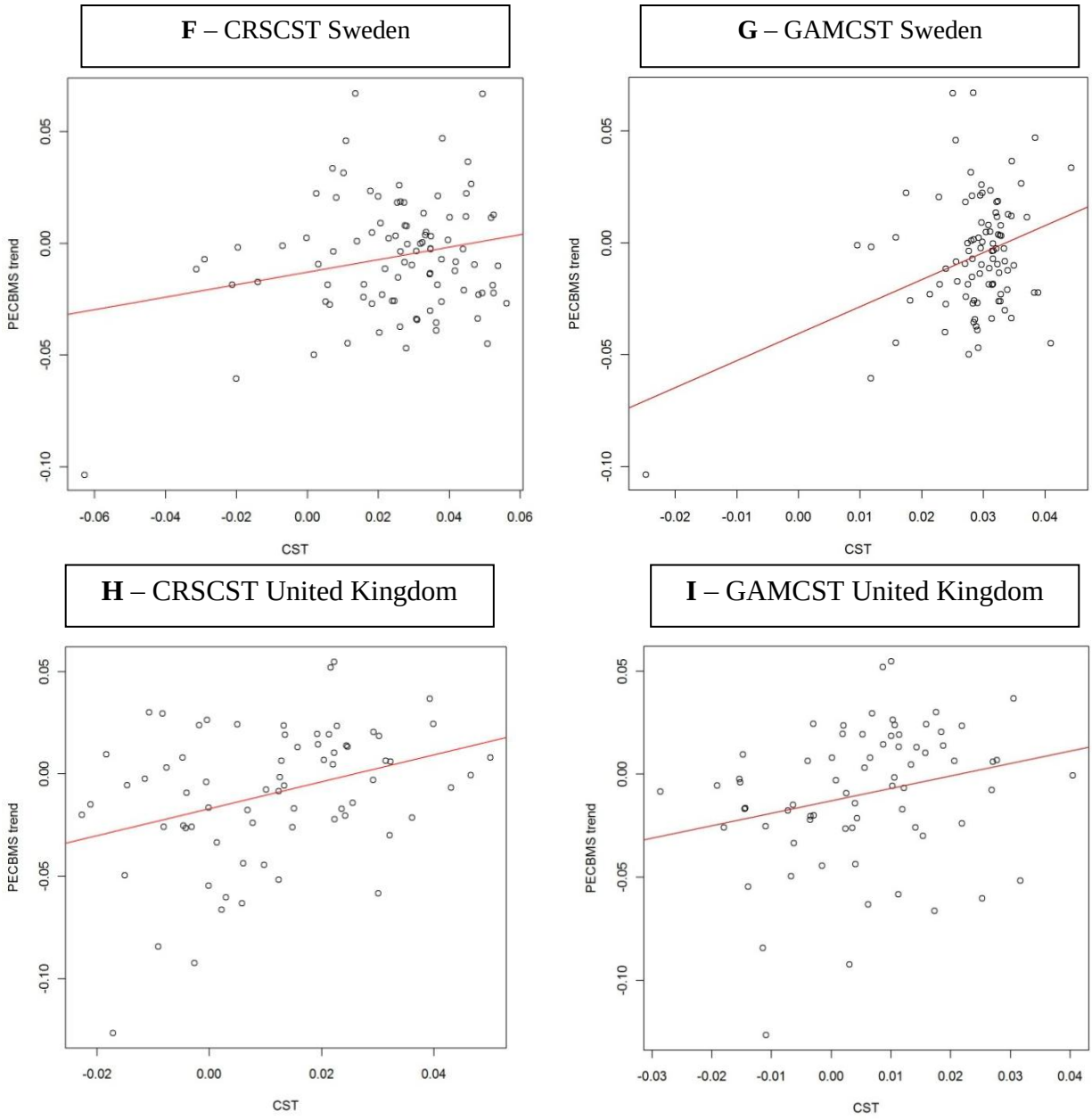


Figure 3.3.1 Continued. The association between CST (CRS and GAM) and PECBMS trend for each country in which the association was significant.

Netherlands was the only country to demonstrate a significant association for GAMCST and not CRSCST (Figure 3.3.1). Of the five countries with positive PECMBS v CST associations, Denmark and Sweden had the strongest, most significant, correlations. In two countries (France, Estonia), PECBMS and CST trend were negatively correlated; however, this was not significant (Table 3.3.1).

Table 3.3.1 Summary of the correlations between CST (CRS and GAM) and PECBMS trends for each country. **Bold** = those countries with a significant positive correlation (Figure 3.3.1) See table 3.2.1 for country codes. r= Pearson's correlation coefficient (between -1 and 1), p= probability the current result would have been found if the correlation coefficient were zero (null hypothesis). If $p<0.05$ the correlation coefficient is statistically significant.

Country	**CRSCST**		**GAMCST**	
	r	**p**	**r**	**p**
BE	0.205	0.107	**0.252**	**0.027**
CH	0.191	0.696	0.167	0.789
CZ	0.012	0.904	0.085	0.390
DE	0.184	0.066	0.160	0.110
DK	**0.381**	**<0.001**	**0.253**	**0.023**
EE	0.053	0.639	-0.204	0.070
FI	-0.010	0.930	-0.004	0.998
FR	0.076	0.478	-0.144	0.178
NL	0.158	0.125	**0.243**	**0.018**
SE	**0.225**	**0.030**	**0.367**	**<0.001**
UK	**0.340**	**0.004**	**0.250**	**0.035**

3.3.2 CST v PECBMS Trends for Individual Species

Of the 109 species examined, the association between CST and the PECBMS trends were positive (CRSCST, 78; GAMCST, 62) more often than negative (CRSCST, 39; GAMCST, 47). However, only 16 species demonstrated a significant association between CST and the PECBMS trend (Appendix Table 6.2). *Oriolus oriolus* had the strongest relationship between CST and the PECBMS trend. Twelve species displayed a significant positive association between CST and PECBMS (*Luscinia luscinia, Hirundo rustica, Oriolus oriolus, Tringa glareola, Picus viridus, Parus caeruleus, Bonasa bonasia, Streptopelia turtur, Garrulus glandarius, Corvus corone, Phoenicurus phoenicurus* and *Oenanthe oenanthe*) and 5 had significant negative associations (*Jynx torquilla, Turdus iliacus, Gallinula chloropus, Merops apiaster* and *Picus viridis*). The

lack of significant correlations between PECBMS trend and CST suggests that other biological factors may be confounding these associations.

3.3.3 Impact of Country Level Monitoring Traits

Neither the duration of monitoring or country size were found to be associated with individual country PECBMS vs CST trends (Figure 3.3.2 and 3.3.3).

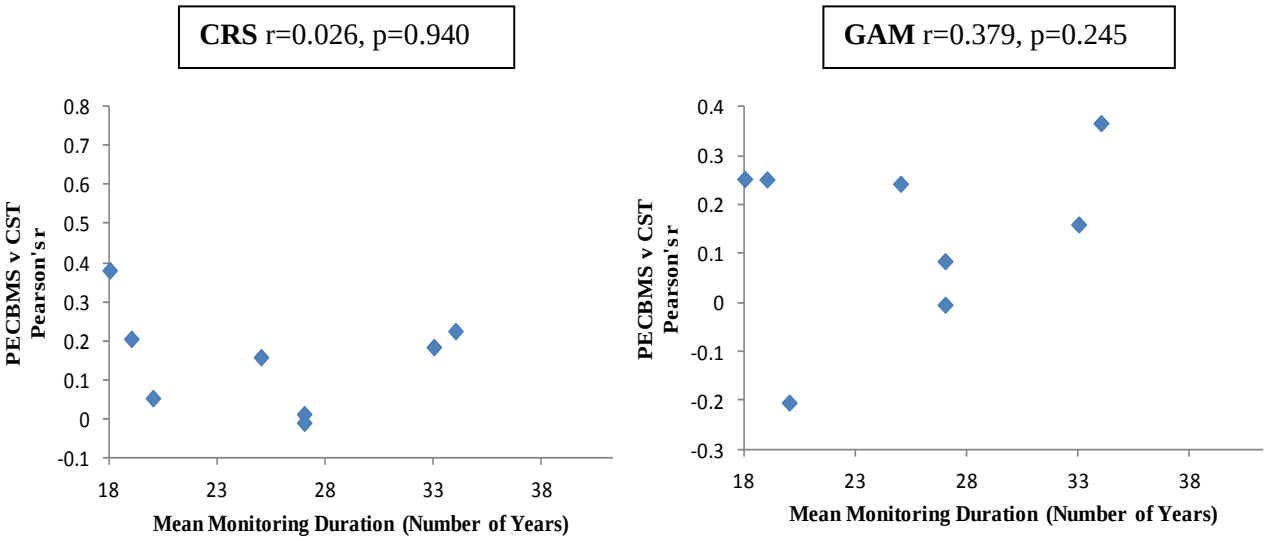


Figure 3.3.2 The association between mean monitoring duration in years and the PECMBS trend v CST (both SDMs) r value for each country.

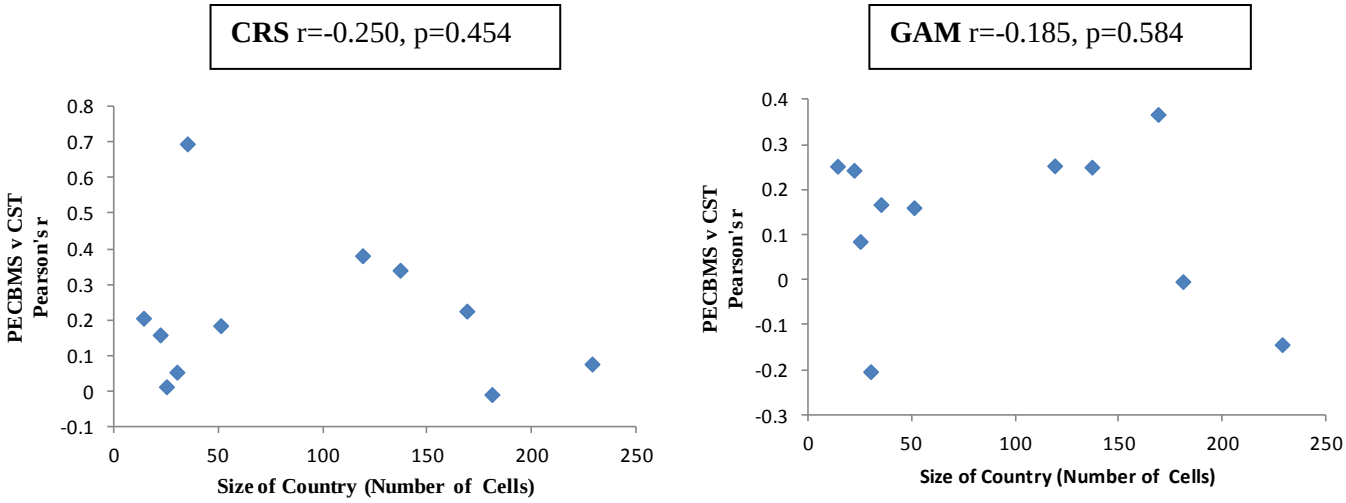


Figure 3.3.3 The association between country size (number of 50km^2 cells within the country) and the PECMBS trend v CST (Both SDMs) r value for each country.

3.3.4 Impact of Species Biological Traits

The ΔAIC scores suggest there that candidate models that incorporate species traits to do not improve the predictive power of CST to explain variation in the PECBMS trend (Table 3.3.4). Richards (2005 and 2008) suggests that models which are merely more complex versions of other models, but with lower ΔAICs, should be ignored. Therefore

the CRSCST model best fits these data, followed by GAMCST. The second models for both model sets (CRSCST+HAB/GAMCST+HAB) are just more complex versions as they include an additional parameter yet do not improve model fit (Table 3.3.4). The effect of CRSCST/GAMCST was well supported regardless of which other variables were included. These results suggest that CRSCST slightly outperforms GAMCST at predicting the PECBMS trend. Furthermore, no other parameter explains a meaningful amount of the remaining variation in the PECBMS trends.

Table 3.3.4 Candidate model set to explain individual species PECBMS trends. Candidate models included all combinations of predictors, including migratory status (MIG), habitat preference (HAB) and log of body mass (LMS) and either CRSCST (A) or GAMCST (B), numbers in brackets = standard error of parameter estimates. Only those with a ΔAIC <=6 are shown.

A)

CRSCST	MIG	HAB	LMS	AIC	ΔAIC	Weight
0.045 (0.016)				-5509.2	0.0	0.3
0.046 (0.016)		+		-5508.0	1.2	0.2
0.045 (0.016)			<-0.000 (0.001)	-5507.2	2.0	0.1
0.045 (0.016)	+			-5507.2	2.1	0.1
0.046 (0.016)	+	+		-5506.2	3.0	0.1
0.046 (0.016)		+	<0.000 (0.001)	-5506.0	3.2	0.1
0.045 (0.016)	+		<0.000 (0.001)	-5505.3	3.9	0.1
0.047 (0.016)	+	+	0.001 (0.001)	-5504.7	4.5	0.0

B)

GAMCST	MIG	HAB	LMS	AIC	ΔAIC	Weight
0.005 (0.031)				-5501.6	0.0	0.4
-0.002 (0.031)		+		-5499.9	1.7	0.2
-0.005 (0.031)			<-0.000 (0.001)	-5499.6	2.0	0.1
-0.001 (0.031)	+			-5499.5	2.2	0.1
-0.002 (0.031)		+	<0.000 (0.001)	-5498.0	3.6	0.1
-0.000 (0.031)	+		<0.000 (0.001)	-5497.6	4.0	0.1
0.004 (0.031)	+	+	0.001 (0.001)	-5496.5	5.2	0.0

3.4 Discussion

The aim of this study was to investigate the use of climatic change as a predictor of population trends and to confirm this by comparing CSTs to the observed population trends in individual countries (the PECBMS trend). Overall it was found that CST is associated with the PECBMS trend only under some circumstances.

The assessment of the association between recent climatic change and population trends at a national scale, reveals that population trend variation in European breeding birds is significantly correlated with the SDM retrodicted trend predictions, associated with climatic change, for 5 of the 11 countries considered. Previous studies (Green *et al.* 2008; Gregory *et al* 2009) have made similar suggestions; that interspecific variation in observed population trends correlates with retrodictions of CST, suggesting that trend predictions produced using the results of SDMs are useful to predict changes in bird populations in a changing climate. The results of this work indicate that investigating such trends at a more restricted, country level can reveal important variations in trends between countries.

It is clear from the CST results produced at country level that not all models produced CST values which were significantly related to the equivalent PECBMS trend (3.3.1); therefore, it is important to question whether these data should be used to create a climate impact indicator. In addition, the precision of calculated CST has previously been questioned due to its sensitivity to extreme annual values of meteorological variables (Gregory *et al.* 2009). Previous papers, (Green *et al.* 2008 and Gregory *et al.* 2009) which have used a similar methodology to that which has been used here, have found that the association between observed population trend and CST was only significant when the effects of potentially confounding variables (biological traits) were taken into account. However, when considering these potentially confounding variables in this work, we have demonstrated that these variables have no significant impact upon the association between PECBMS and CST. Furthermore, Gregory *et al.* (2009) suggest the association between their population trend and calculated CST is near-significant across Europe. However, from this investigation it is clear that the association between population trend and CST varies significantly between countries and, although not significant, the association between these CST and the PECBMS trend in some countries is actually negative (3.3.1). Therefore, the grouping of countries to create European CSTs masks these associations occurring within individual countries.

Overall, CSTs derived from SDMs of European breeding distributions of birds demonstrated some associations with observed population trends (the PECBMS trend); although there was considerable unexplained variation and not all effects were statistically significant. Green *et al.* (2008) found that the effect of CST was most apparent when the rarest species were excluded. They suggested that this may be due to the vulnerability of very small populations to stochastic effects. Furthermore, Gregory *et al.* (2009) excluded population trends for two raptors (common buzzard, *Buteo buteo*, and Eurasian sparrowhawk, *Accipiter nisus*) whose populations had been heavily influenced by pesticide poisoning in the 1950 – 60s, and continued human persecution. No species were excluded, based on rarity or external population influences, from the analyses reported in this chapter. Excluding these species may have increased the relationship between observed population trend (the PECBMS trend) and CST.

As discussed in Chapter 2, the effect of climatic change on bird populations may not necessarily be direct. Climate may impact upon habitat quality and food sources which indirectly affects population responses to climatic change (Both *et al* 2006; Holmes

2007; Treinys *et al*. 2008). However, species richness is also affected by factors other than climate. Factors which have not been considered here, such as the effect of non-breeding climate suitability, density-dependence, migratory route changes, breeding success, competition and predation (Beale *et al.* 2006, Lemoine and Bohning-Gaese 2003, Holmes 2007, Newton 2006), could be included in future research to further investigate the impact of these variables on population trends. The exploration into the relationship between CST and the PECBMS trend demonstrates the uncertainty surrounding these methods of calculating species distribution and climatic suitability, which warrant further investigation.

Here, I attempted to take into account the effects of varied levels of monitoring. Of the monitoring variables considered, the countries which demonstrated an overall significant relationship between CST and the PECBMS trend were of varied size and monitoring duration (i.e. both BE and UK were significant with country size and monitoring durations of 15 cells, 18 years and 137 cells, 41 years respectively). Therefore, it was expected that the monitoring variables would have a minimal impact upon the CST v PECBMS trend, which was demonstrated in section 3.3.3. Although no significance was demonstrated in the relationship between length of monitoring and CST v PECBMS trend relationship, the importance of using data collection periods which have run for as long as possible is key to ensure accurate trend calculations. Over time, as more data are collected on a wider scale, these calculations will continue to improve (Nichols and Williams 2006).

The relationship demonstrated between CST and the PECBMS trends at a national scale indicates that factors other than climate may be affecting and constraining species' populations. Overall, model selection indicated very little support for the role of biological variables as none of the variables featured in the 'best' model. However, each of the three biological variables did feature in the first 5 models for both CRSCST and GAMCST.

Despite limitations, the results of this study are encouraging and indicate that SDMs can demonstrate relevant changes in climate that are affecting species to some extent. The assessment of the true effect of climate on European bird populations is made more difficult by the weak climatic trends during the limited time period covered by some countries' PECBMS trend data. However, future climatic change is predicted to be

more severe and this may enable the demonstration of a more direct link between population trends and climatic suitability (IPCC 2007).

There remains unexplained variance in the dataset as to the driver behind population change. However, despite the relative coarseness of the data, these results suggest that there is a detectable climate signal in the population trends within some individual countries. This provides a valuable validation of the use of SDMs, both to study the potential impacts of future climatic changes (Huntley *et al.* 2007, 2008), and to produce indicators of the impacts of climatic change on biodiversity (Gregory *et al.* 2005, Green *et al.* 2008).

3.5 References

Araújo, M. B. and Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*. **16** 743–753

Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19** 716-723

Anderson, D.R. (2008) *Model based inference in the life sciences: a primer on evidence*. Springer, New York

Arguez, A, and Vose, R. (2011) The definition of the standard WMO climate normal: the key to deriving alternative climate normals. *Bulletin of the American Meteorological Society*. **92** 699–704

Barton, K. (2009) MuMIn: multi-model inference. R package, version 1.7.2. Available at: http://r-forge.r-project.org/projects/mumin/

Beale, C.M., Burfield, I.J., Sim, I.M.W., Rebecca, G.W., Pearce-Higgins, J.W. and Grant, M.C. (2006) Climate change may account for the decline in British ring ouzels *Turdus torquatus. Journal of Animal Ecology* **75** 826-835

Behrens, A., Georgiev, A. and Carraro, M. (2010) *Future impacts of climate change across Europe*. CEPS Working Document No. 324

Both, C., Bouwhuis, S., Lessells, C.M., and Visser, M.E. (2006) Climate change and population declines in a long-distance migratory bird. *Nature* **441** 81-83

Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J. and Foppen, R.P.B. (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of The Royal Society B Biological Sciences* **277** 1259-1266

Burnham, K.P. and Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd Ed. Springer-Verlag, New York, New York 488

Caro, T.M. and O'Doherty (1999) On the use of surrogate species in conservation biology. *Conservation Biology* **13** 805-814

Foden, W., Mace, G., Vié, J.-C., Angulo, A., Butchart, S., DeVantier, L., Dublin, H., Gutsche, A., Stuart, S. and Turak, E. (2008) Species susceptibility to climate change impacts. 77–87 in Vié, J.C., Hilton-Taylor, C. and Stuart, S.N eds Wildlife in a changing world: an analysis of *the 2008 IUCN Red List of threatened species*. Gland, Switzerland: IUCN

Green, R.E., Collingham, Y.C., Willis, S.G., Gregory, R.D., Smith, K.W. and Huntley, B. (2008) Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters* **4** 599-602

Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B. and Gibbons, D.W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **360** 269–288

Gregory, R.D., Vorisek, P., Strien, A.V., Meyling, A.W.G., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P. and Burfield, I.J. (2007) Population trends of widespread woodland birds in Europe. *Ibis* **149** 78-97

Gregory, R.D., Vorisek, P., Noble, D.G., van Strien, A.J., Pazderová, A., Eaton, M.E., Gmelig., Meyling, A.W., Joys, A., Foppen, R.P.B. and Burfield, I.J. (2008) The generation and use of bird population indicators in Europe. *Bird Conservation International* **18** S223–S244

Gregory, R.D., Willis, S.G., Jiguet, F., Vorisek, P., Klvanova, A., Van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D. and Green, R.E. (2009) An indicator of the Impact of Climatic Change on European Bird Populations. *PLoS one* **4** 1-6

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. and Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12** 450-455

Hill, J.K., Thomas, C.D. and Huntley, B. (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London* **266** 1197-206

Holmes, T.R. (2007) Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. *The International Journal of Avian Science* **149 s2** 2-13

Huntley, B., Green, R. E., Collingham, Y. and Willis, S. G. (2007). *A climatic atlas of European breeding birds*. Durham, Sandy and Barcelona: Durham University, RSPB and Lynx Editions.

Huntley, B., Collingham, Y.C., Willis, S.G. and Green, R.E. (2008) Potential impacts of climatic change on European breeding birds. *PLoS ONE* **3** e1439

IPCC (2007), Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., and Miller, H.L. (eds.) *Climate change 2007: the physical science basis*, contribution of working group I to the **Fourth Assessment Report** of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

IUCN (2002) *2002 IUCN Red List of threatened species.* Gland: IUCN www.redlist.org Accessed 05/05/11

Johnson, J.B. and Omland, K.S. (2004) Model selection in ecology and evolution. *TRENDS in Ecology and Evolution* **19** 101-108

Jones, J.P.G. (2011) Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology* **48** 9-13

Julliard, R., Jiguet, F. and Couvet, D. (2003) Common birds facing global changes: what makes a species at risk? *Global Change Biology* **10** 148-154

Lemoine, N. and Böhning-Gaese, K. (2003) Potential impact of global climate change on species richness of long-distance migrants. *Conservation Biology* **17** 557-586

Mazerolle, M.J. (2006) Appendix 1: Making sense out of Akaike´s information criterion (AIC): its use and interpretation in model selection and inference from ecological data. http://www.theses.ulaval.ca/2004/21842/apahtml 1-12 Accessed 07/05/11

McCarty, J.P. (2001) Ecological consequences of recent climate change. *Conservation Biology* **15** 320-331

McRae, B.H., Schumaker, N.H., McKane, R.B., Busing, R.T., Solomon, A.M. and Burdick, C.A. (2008) A multi-model framework for simulating wildlife population response to land-use and climate change. *Ecological Modelling* **219** 77-91

Newton, I. (2006) Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology* **147** 146-166

Nichols, J.D. and Williams, B.K. (2006) Monitoring for conservation. *Trends in Ecology and Evolution* **21** 668-673

Osborne, P.E., Alonso, J.C. and Bryant, R.G. (2001) Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology* **38** 458-471

Renwick, A.R., Massimino, D., Newson, S.E., Chamberlain, D.E., Pearce-Higgins, J.W. and Johnston, A. (2012) Modelling changes in species' abundance in response to projected climate change. *Diversity and Distributions* **18** 121-132

Richards, S.A. (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* **86** 2805-2814

Richards, S.A. (2008) Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology* **45** 218-227

Richards, S.A., Whittingham, M.J. and Stephens, P.A. (2011) Model selection and model averaging in behavioral ecology: the utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology* **65** 77-89

Sæther, B. (2000) Weather ruins winter vacations. *Science* **228** 1975-1976

Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. and van Bommel, F.P.J. (2006) Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation* **131** 93-105

Sekercioglu, C.H., Schneider, S.H., Fay, J.P. and Loarie, S.R. (2008) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* **22** 140-150

Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P. and Wilson, J.D. (2000) The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. *Journal of Applied Ecology* **37** 128-148

Snow, D.W. and Perrins, C.M. (1998) The birds of the Western Palearctic: Concise edition. Oxford University Press, Oxford

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L. and Williams, S. E. (2004) Extinction risk from climate change. *Nature* **427** 145–148

Treinys, R., Lõhmus, A., Stončius, D., Skuja, S., Drobelis, E., Šablevičius, B., Rumbutis, S., Dementavičius, D., Naruševičius, V. and Petraška, A. (2008) At the border of ecological change: status and nest sites of the Lithuanian Black

Stork *Ciconia nigra* population 2000-2006 versus 1976-1992. *Journal of Ornithology* **149** 75-81

Chapter 4 - Developing Climatic Change Indicators for European Birds at a National and Regional Level

4.1 Introduction

Landres *et al.* (1988) provided a clear definition of an indicator species: "*an organism whose characteristics (e.g. presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest*".

Indicator species are used to demonstrate the average trends in abundance of a selected set of species. Biodiversity indicators are important in conservation and have been used to show changes in the condition of ecosystems; something that is difficult and expensive to measure directly (Duelli and Obrist 2003; Kati *et al.* 2004; Mace and Baille 2007; Butchart *et al.* 2010). Many benefits are associated with using common bird data to produce such biodiversity indicators; these include the straightforward nature and low cost of data collection methods, use of existing data, ease of communication, and ease of update (Gregory *et al.* 2003). Common bird indicators can help to measure progress towards reducing the rate of biodiversity loss at the national, regional and global levels. The use of indicators is becoming increasingly common as policy makers struggle to ensure the preservation and enhancement of biodiversity (Lindenmayer *et al.* 2000). An example of an indicator produced on a national scale to inform policy is the UK common bird indicator. This index is based upon the population trends of common UK breeding birds from 1970 onwards and demonstrates that common birds have increased by an average of 10% over the period 1970-2002, whereas farmland and woodland bird populations have fallen by 42% and 15%, respectively, over the same period. This indicator was adopted by the UK government as a headline indicator of the sustainability of lifestyles in the UK (Defra 2012). As a result of the index, the government adopted a formal agreement to reverse the decline in the number of farmland birds by 2020 (Gregory *et al.* 2004). This agreement led to a change in both agricultural production and land-use policy to ensure biodiversity is maintained and restored (Birdlife 2010).

The Pan-European Common Bird Indicator is an example of an indicator produced at a European level (Gregory *et al.* 2005), and which assesses breeding bird population trends across 18 European Countries. This indicator revealed that common farmland

birds in Europe had declined steeply over the last 20 years, whereas common woodland birds had not. This farmland bird index has now been formally adopted by the European Union as a Structural Indicator for Europe (Birdlife 2010). Bird trends have also been used to monitor progress towards policy goals. For example, in Northern French Guiana, population trends of forest-dependent bird species have been used to monitor the level of habitat degradation and the extent of recovery of forests that are under restoration (Thiollay 1997).

The maintenance of diversity of living systems is critical for ecosystem functioning. However, the accelerating pace of global change is threatening the preservation of biodiversity (Chiarucci *et al.* 2011). A wealth of evidence suggests that one driver responsible for a large percentage of recent changes in levels of biodiversity is the rapid rate of anthropogenic climatic change (Walther *et al.* 2002; Root *et al.* 2003; Parmesan and Yohe 2003; Julliard *et al.* 2004). The use of SDMs to project the potential impact of climatic change on bird populations equips management teams with critical information to inform management decisions and policy (Butchart *et al.* 2010; Jones 2011). Birds are often used as indicator species to track the progress towards conserving biodiversity as they integrate multiple environmental changes due to their mobility and often wide ranges (Hansson 1998). Such indicators can be calculated by combining species distribution model (SDM) projections of the impact of climatic change on bird distributions, with systematic bird population monitoring, to illustrate the effects of climatic change on biodiversity.

This type of integration was undertaken by Gregory *et al.* (2009) to produce a Climatic Impact Index for European birds. Their index combines data from those species expected to gain or lose range in response to climatic change, and demonstrates the increasing impact climatic change has had on European birds over the last twenty years (Figure 4.1.1).

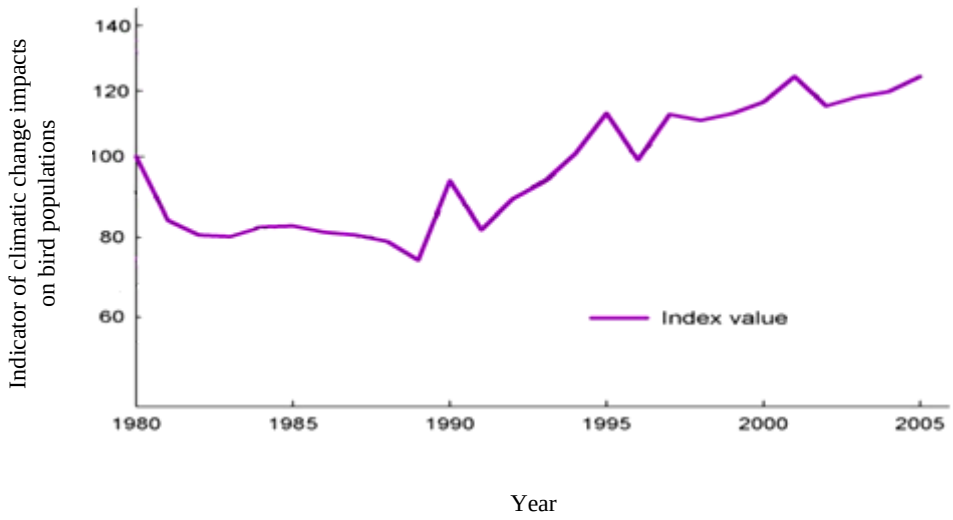


Figure 4.1.1 The Climatic Impact Indicator produced by Gregory *et al.* (2009). The indicator shown is calculated as the ratio of two population indices (with the indicator set to 100 at 1980): one for European bird species whose potential geographical ranges are expected to expand under projections of future climatic change and a second for those species projected to contract their range due to future climatic change.

Bird population trends vary greatly across Europe and trends in different parts of Europe may be affected by different mechanisms (Tucker *et al*. 1997). Europe consists of a varied range of habitats and climates and projected climatic changes are not uniform across the continent. As climate changes, species will respond to these regional, spatially heterogeneous climatic changes and not to global average climatic change (Torti and Dunn 2005). Therefore, populations of a single species may alter in different ways across their European range as climates change. As a result, a climatic change indicator that aggregates population trends over the entire continent may mask climatic change impacts that affect populations differently across a species' range. For example, the northern European range of a species may be increasing due to the availability of suitable climate, whereas the southern range may be decreasing due to a lack of suitable climate. An aggregated European climatic change indicator may suggest the trend for this species is stable, whereas climatic change indicators produced at regional/national scales would be capable of revealing the differences between northern and southern trends. To further knowledge and understanding of the processes involved in population responses to climatic change, here I examine population trends within more restricted parts of species' ranges. Studying population trends at a national scale enables more accurate population management (i.e. management of biodiversity within a country rather than across the entire continent). However, as national trends could also be affected by the quality of population trend data collected (see 3.3.3), regional trends may provide a more robust signal of species response to climate. For this reason, here I

also consider regional indicators. Investigating population trends and climatic suitability at a regional level may enable a clearer analysis of the relationship between climate and population trends.

It is expected that countries and regions with longer periods of population monitoring will provide clearer indications of the impact of climate upon populations (i.e. those species for which climate is deteriorating experiencing population decreases and those species for which climate is improving experiencing increases in population trend).

This chapter uses SDMs fitted to climatic data to investigate how European bird populations have been affected by changing climatic suitability. Climatic Impact Indicators (CII) are produced at national and regional spatial scales, based upon the divergence in population trends between species expected to be positively and negatively affected by climatic change, following the approach of Gregory *et al.* (2008). Finally, I produce CIIs for individual European bird species across Europe, using a similar method to the country and regional analyses but assigning individual countries into one of two groups for a species, according to the change in climate suitability for single species. I also investigate whether species biological traits (habitat preference, migratory status and mass) affect individual species' CII slopes.

4.2 Methods

Selection of Data

Trends for 145 bird species monitored across Europe (Table 3.2.2) were included in our analyses. These data were derived from annual breeding bird monitoring schemes in 20 European countries (PECBMS: http://www.ebcc.info/pecbm.html) (Table 3.2.1).

All 20 European countries partaking in the PECMBS were included (Table 3.2.1). Each country was allocated to a single region, following PECBMS classification (Table 4.2.1).

Table 4.2.1 The allocation of individual countries into area of Europe for regional trend analyses. Species distribution and bioclimatic data for West and East Germany were separated.

North	East	South	West
Sweden	Estonia	France	Ireland
Finland	Latvia	Spain	UK
Norway	Poland	Italy	Netherlands
	Czech Republic		Denmark
	Hungary		Austria
	East Germany		Switzerland
			Belgium
			West Germany

The three bioclimatic variables used to relate species ranges to climatic suitability, and subsequently to estimate annual climate suitability at sites, were the same as used in earlier chapters (2.2.1): annual temperature sum above 5°C (GDD5), mean temperature of coldest month (MTCO), and an estimate of the annual ratio of actual to potential evapotranspiration (AET/PET). The climate data were obtained from CRU TS 3.1 (www.badc.nerc.ac.uk).

Producing Multispecies Population Indices (National and Regional)

SDMs were fitted to the European atlas data for each of the 145 PECBMS species (supplemented with digitised data for species ranges in Turkey, Cyprus and North Africa – see Chapter 2 for further information) using the 30 year (1960-1990) CRU derived bioclimatic data. The resultant models were then applied to the annual bioclimatic data (also from CRU) from the first year of PECBMS monitoring in each country (which varied among countries; Table 3.2.1), up to 2009, to simulate climatic suitability for each bird species, in each 50km cell, in each country. For each species within a country, the mean suitability of all cells for each year was then calculated. Logit-transformed annual mean suitabilities were regressed against time; the slope of this relationship is referred to as the Climate Suitability Trend (CST) – as presented and discussed in Chapter 3.2.

In this chapter, CST values for individual species are used to partition all species into two groups, termed CST+ and CST- species; assignment to a group depends upon the sign of a species' CST over the period of monitoring in a focal region. This was done for all species in each country and for each of four European sub-regions (Table 4.2.1).

Separate indices were calculated for the CST+ and CST- groupings (methods below). The methods used closely follow those described by Gregory *et al.* (2009). However, in contrast to the continent-wide indices developed by Gregory *et al.* (2009), here CSTs and indices are downscaled and calculated on a national and regional scale.

All species with positive CST trends were grouped as CST+ and all species with negative CST trends were grouped as CST- (no species' CST value was exactly zero). This process was undertaken separately for CST data produced by the two SDM methods (generalised additive model (GAM) and climate response surface (CRS); see Chapter 2) to produce two sets of indices. The initial value of the index was always set at 100 for the first monitoring year. This process was repeated using the regional population trend (from PECBMS) and calculating annual mean SDM suitabilities for all 50km cells across each region. If climatic change was driving bird population trends in the manner predicted, we would expect CST+ indices to increase and CST- indices to decline.

Producing Indicators (National and Regional)

Considered separately, the indices (CST+ and CST-) produced for the two groups of species do not equate to an indicator of the impact of climatic change upon the population trends of European birds as both groups may be similarly susceptible to non-climatic environmental pressures, such as habitat loss or agricultural intensification and, for example, may decline at similar rates if climatic change had no effect (Gregory *et al.* 2009). To produce climatic change indicators for each country and region, a geometric mean of the PECBMS index for individual species in a year was calculated separately for the CST+ and CST- species indices, with the contribution of each species PECBMS index to the geometric mean weighted by the absolute value of CST, for that species. The process was undertaken separately for CST values derived from GAM and CRS modelling methods.

The calculation of this indicator rested upon the expectation that a projection of expansion of potential geographical range (nationally and regionally) is likely to be associated with increased breeding population, and vice versa. Annual values of the CII were calculated as the ratio of the index for CST+ species to CST- species in each year (after Gregory *et al.* 2009). A calculated CII with a slope of zero indicates that climatic change is having no effect upon trends. This slope was used to determine whether the trends are diverging as expected. As national and regional CIIs of bird population

increase in value, this demonstrates increased conformity to the predicted population response to climatic change.

Producing Individual Species Indicators

To calculate individual species' indices, rather than grouping the species into CST+ and CST- for a country or region, countries were assigned into CST+ and CST- groups for a species, defined by that species' trend in different countries. Specifically, when the CST for a species in a country was positive, that country was allocated to the CST+ group; countries where the species' CST was negative were allocated to the CST- group. A CII could then be estimated for an individual species by separately taking the weighted geometric mean of PECBMS trends in the CST+ and the CST- groups and calculating the ratio of these two values. Individual species' CIIs were produced only when data were available from at least four countries (98 species satisfied this criterion). As with the country and regional analyses, the initial value of the CII was set to 100 in the first year when data for a minimum of four country PECBMS indices were available. These analyses were undertaken separately for CST values derived from GAM and CRS models.

Individual species' CIIs were further examined, using analysis of covariance (ANCOVA), to determine whether a number of species' biological traits could account for variation in population responses to recent changes in climate. Traits considered were migratory status (with species defined as long distance migrants, short distance migrants or resident) and habitat preference (with species being allocated into one of three principal habitat preferences: farmland, woodland or other) – for further discussions of these groupings see 3.2.4. GLMs were run using R (R Development Core Team, 2011) with the slope of the individual species' CII as the predictor variable and the biological traits of each species as potential explanators of the variation in CIIs.

CRS and GAM SDMs were both used to produce CIIs of national, regional and individual species responses. However, for simplicity (and as results from the two SDM methods were similar), only the plots produced by CRS are included in this chapter (results for GAMs are included in appendix 6.2).

4.3 Results

4.3.1 Country Indices and CII

Countries with longer time series (>20 years) show the expected diverging trends of CST+ and CST-, the former positive, the latter negative (Figure 4.3.1). In countries with shorter time series (<12 years) there was, as predicted, no consistent pattern of trend data (Figure 4.3.2). However, annual CIIs for countries with a shorter time series have a much smaller range than those of countries with a longer time series (Figure 4.3.1 and 4.3.2). There is a clear relationship between duration and CII slope after the exclusion of Latvia, an obvious outlier, ($F=17.372$ $R^2=0.521$ $p=<0.001$ Standard Error=7.364; Figure 4.3.3), with CII slopes being steeper in countries with longer monitoring.

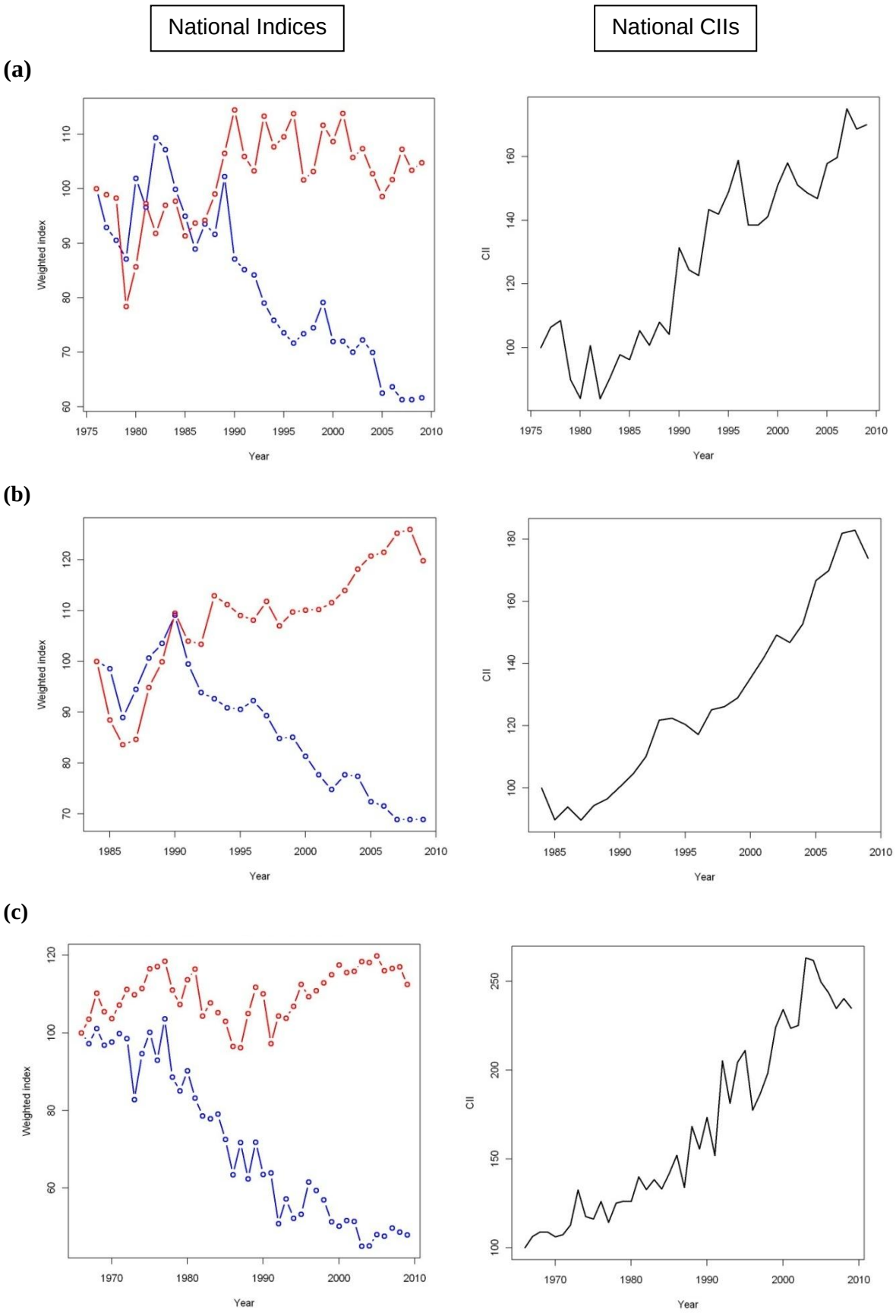


Figure 4.3.1 Examples of CST+, species with a positive CST (red line) and CST-, species with a negative CST (blue line) weighted indexes (left-hand plots); and corresponding CIIs (right-hand plots) for three countries with >20 years of species trend data. Number of species in each category: **(a)** Denmark CST+ 59, CST- 21, **(b)** Netherlands CST+ 59, CST- 37, **(c)** United Kingdom CST+ 55, CST- 26.

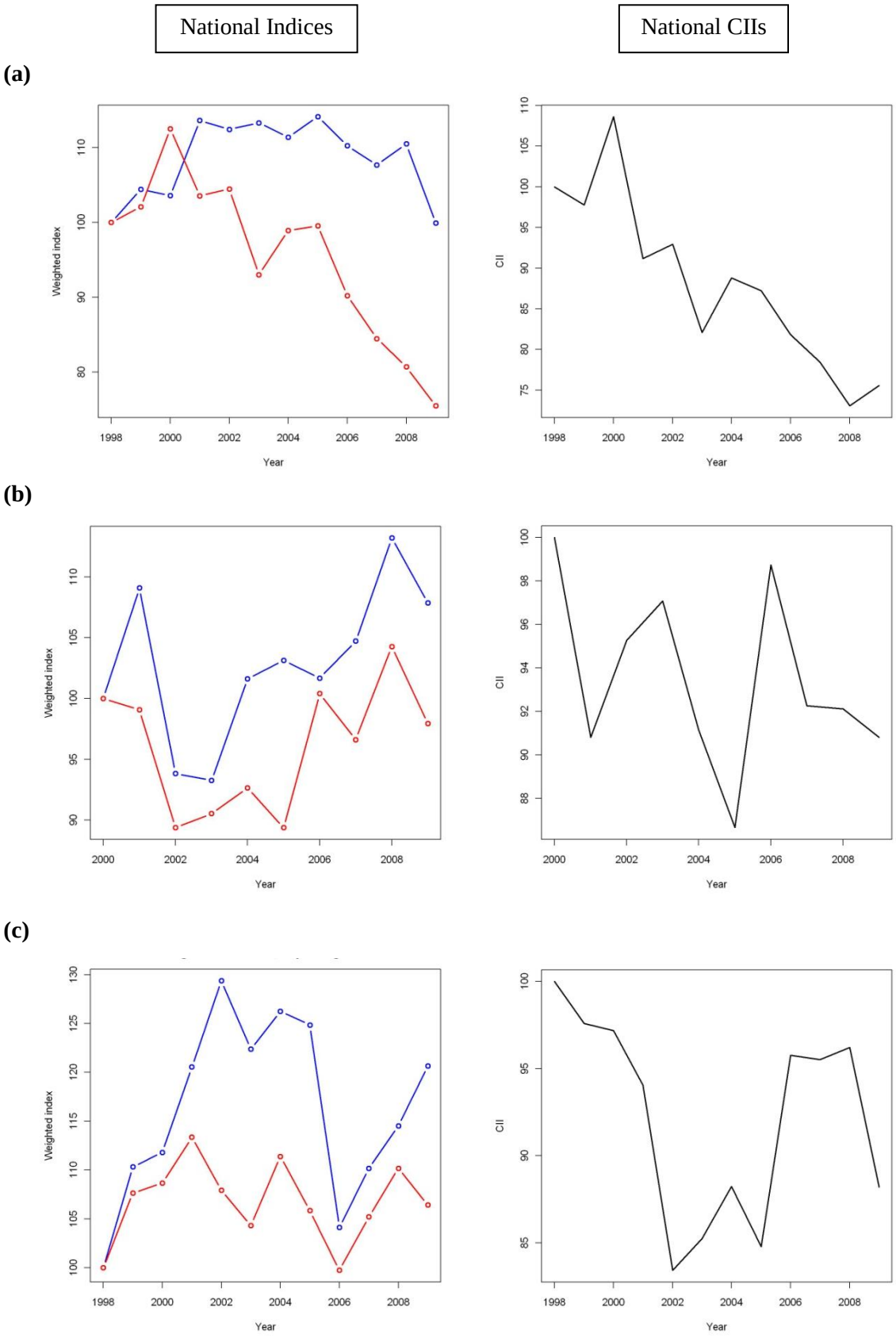


Figure 4.3.2 Examples of CST+, species with a positive CST (red line) and CST-, species with a negative CST (blue line) weighted indexes (left-hand plots); and corresponding CIIs (right-hand plots) for three countries with ≤14 years of species trend data. Number of species in each category: **(a)** Austria CST+ 42, CST- 37, **(b)** Poland CST+ 17, CST- 87, **(c)** Spain CST+ 85, CST- 11.

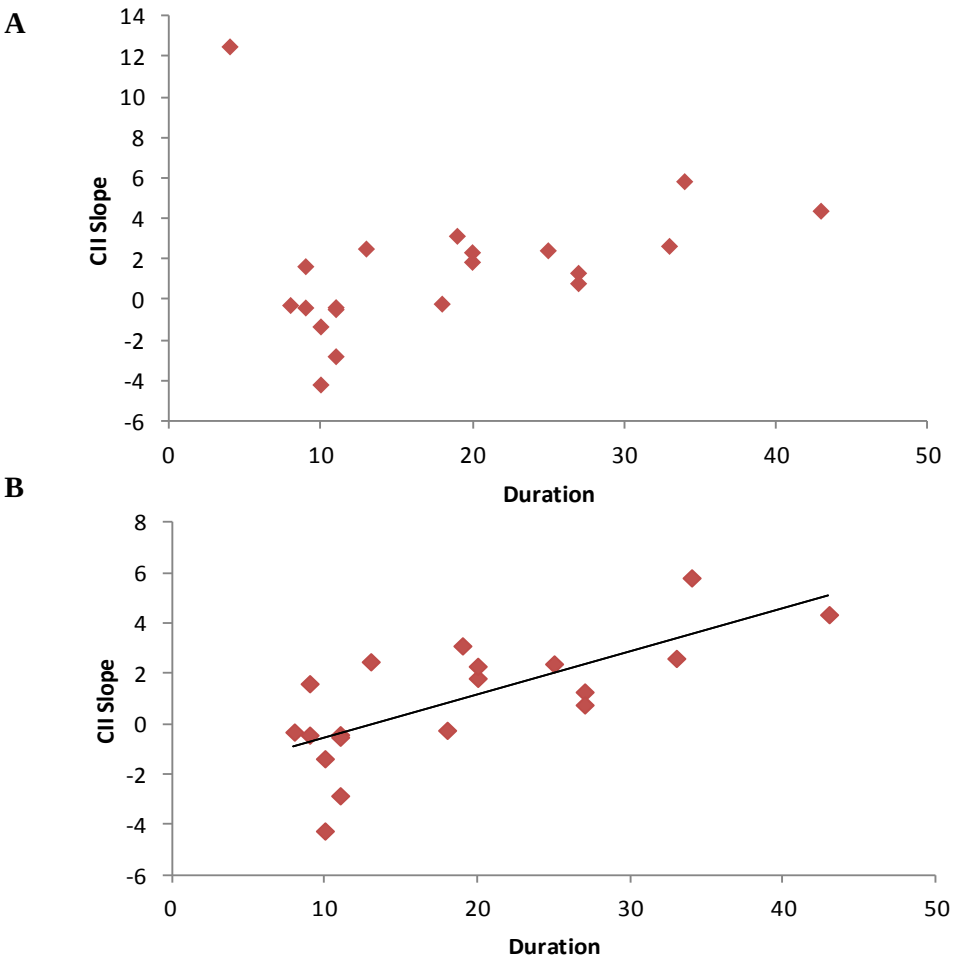


Figure 4.3.3 CII slope against monitoring period from all PECMBS countries where national indicators where calculated. **A**– All country data y=0.0773x + 0.1316 F=0.679 R^2=0.038 p=0.421 Standard Error=10.718, **B** – All country data excluding Latvia y=0.1726x - 2.2963 F=17.372 R^2=0.521 p=<0.001 Standard Error=7.364.

4.3.2 Regional Indices and CIIs

There is a strong climatic signal when CIIs are calculated at a regional scale; three of the four regional CIIs produced are in the expected direction (Figure 4.3.4). The one regional CII which does not display the expected impact of climate is that for southern Europe. Here, the CST+ index declines rapidly over the first five years, which appears to drive the CII signal. Trend data were only available for three countries and only for a duration of 19 years in southern Europe, whereas all other regions have trend data spanning over 25 years. The three regions which show a clear effect of climatic change (east, north and west Europe –Figure 4.3.4) indicate that the impact of climate has increased greatly over the past 20 years (steeper CII trends), which coincides with a period of rapid warming (Trenberth *et al.* 2007).

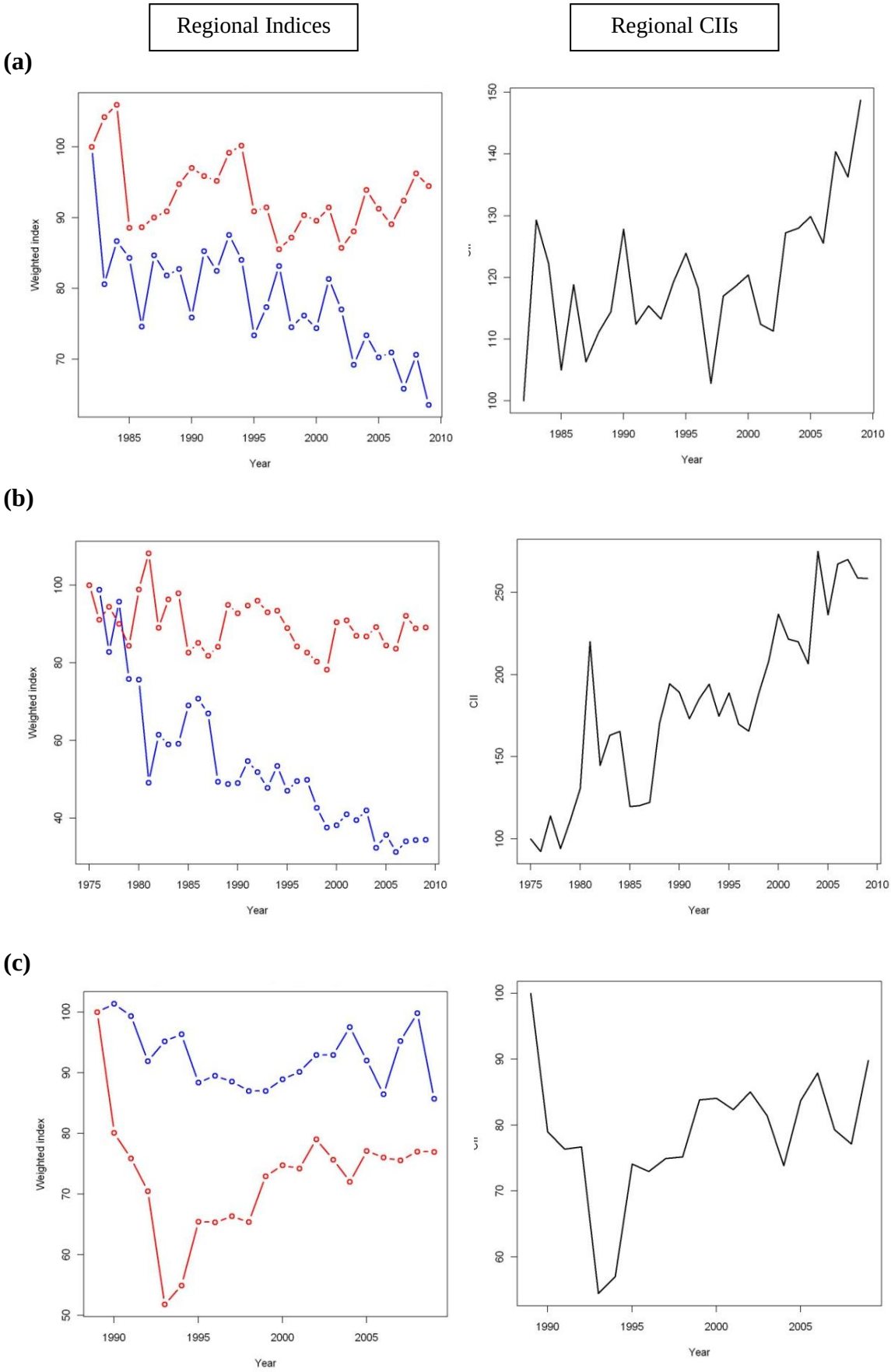


Figure 4.3.4 Regional indices; CST+, species with a positive CST (red line) and CST-, species with a negative CST (blue line) weighted indexes (left-hand plots); and corresponding CIIs (right-hand plots) for each region. Number of species in each category: **(a)** East Europe CST+ 73, CST- 31, **(b)** North Europe CST+ 85, CST- 11, **(c)** South Europe CST+ 28, CST- 88, **(d)** West Europe CST+ 63, CST- 40.

(d)

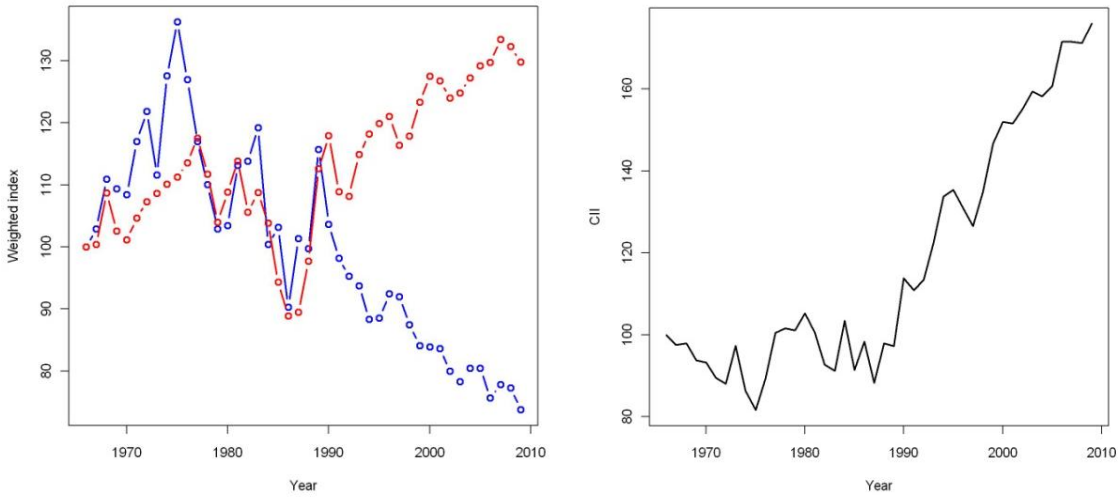


Figure 4.3.4 Continued. Regional indices; CST+, species with a positive CST (red line) and CST-, species with a negative CST (blue line) weighted indexes (left-hand plots); and corresponding CIIs (right-hand plots) for each region. Number of species in each category: **(a)** East Europe CST+ 73, CST- 31, **(b)** North Europe CST+ 85, CST- 11, **(c)** South Europe CST+ 28, CST- 88, **(d)** West Europe CST+ 63, CST- 40.

4.3.3 Producing Species Indices and CIIs

Of the CIIs produced for individual species there are examples of negative, positive and limited differential population responses among countries relating to recent climatic change (Table 4.3.2, Figures 4.3.5 – 4.3.7). A Chi-squared test comparing the number of species with a positive, neutral and negative CII trends (>0.5, between 0.5 and -0.5, or <-0.5) suggested no particular bias towards one of these categories ($\chi 2_{2,\ 98}$=3.50, p=0.17). Furthermore, no significant relationships were found between the biological traits investigated and species' CII slopes (Table 4.3.3).

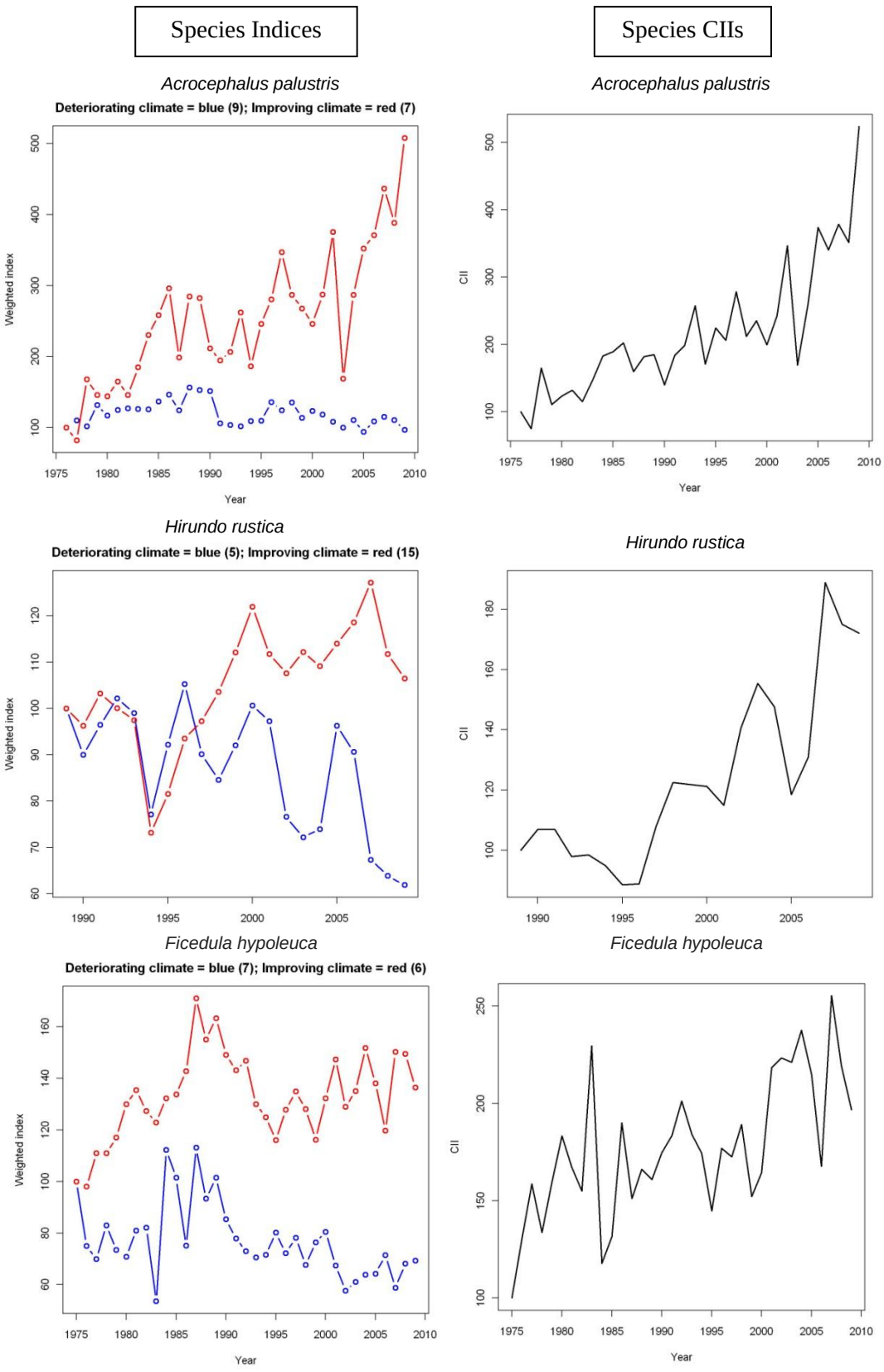


Figure 4.3.5 Examples of CST+ (red) and CST- (blue) indices (left) and corresponding CIIs (right) from a selection of species which displayed a climatic signal in bird population trends, in the expected direction (i.e. the CST+ index shows an increase in countries in which climate has become more suitable and CST- species decreasing as climate suitability has deteriorated).

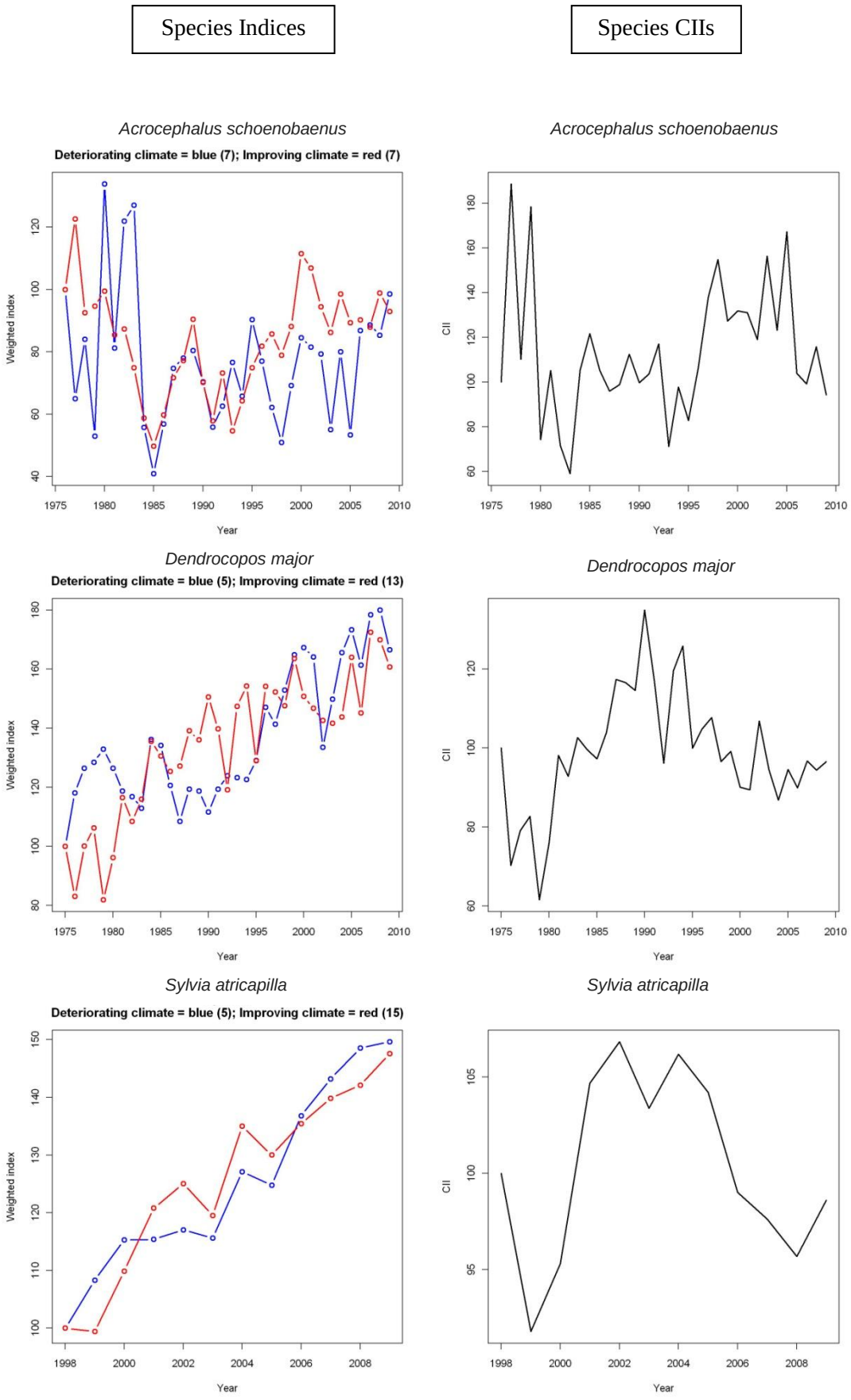


Figure 4.3.6 Examples of CST+ (red) and CST- (blue) indices (left) and corresponding CIIs (right) from a selection of species which displayed no climatic signal in bird population trends (i.e. CST+ and CST- species' trends remain similar as climate changes).

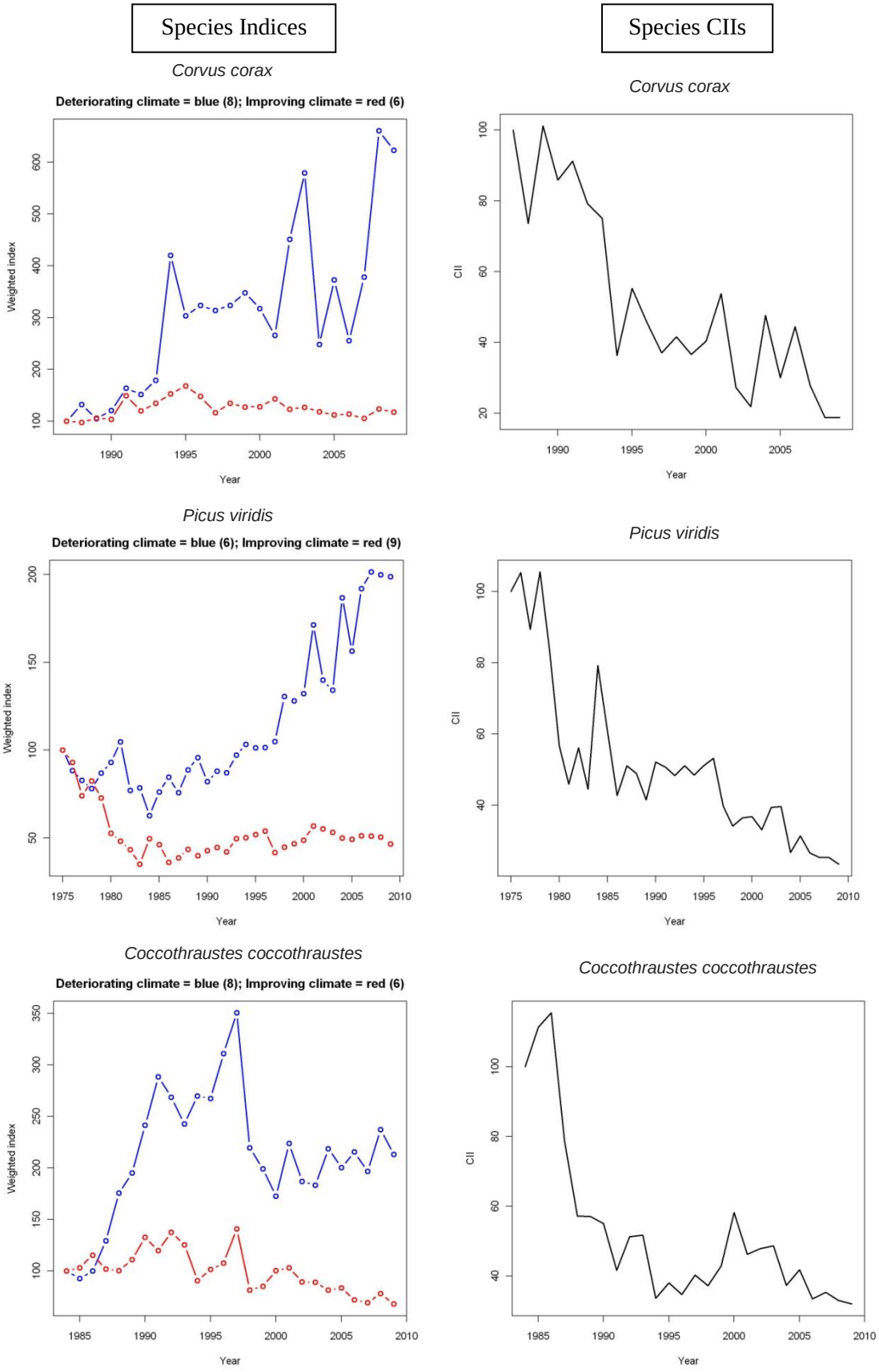


Figure 4.3.7 Examples of CST+ (red) and CST- (blue) indices (left) and corresponding CIIs (right) from a selection of species which displayed the opposite to the expected climatic signal in bird population trends (i.e. CST+ species decreasing as climate is more suitable and CST- species increasing as climate suitability deteriorates).

Table 4.3.2 Individual species' descending CII slopes (following Gregory *et al* 2009). Values below -0.5 demonstrate species responding opposite to expected in response to climate, between -0.5 and 0.5 no impact of climatic signal and above 0.5 species displaying the expected climatic signal –designated as close to zero and therefore unlikely to reflect strong climatic impacts.

Species	**CII slope**	**Species**	**CII slope**
Motacilla flava	31.812	*Phoenicurus phoenicurus*	-0.013
Passer montanus	24.318	*Corvus corone*	-0.021
Oriolus oriolus	15.457	*Parus cristatus*	-0.227
Oenanthe oenanthe	10.867	*Anthus trivialis*	-0.334
Vanellus vanellus	9.053	*Sitta europaea*	-0.421
Acrocephalus palustris	8.057	*Parus montanus*	-0.481
Sylvia communis	5.681	*Fringilla coelebs*	-0.49
Motacilla alba	4.006	*Pica pica*	-0.503
Hirundo rustica	3.947	*Delichon urbica*	-0.673
Turdus pilaris	3.403	*Dryocopus martius*	-0.734
Hippolais icterina	3.039	*Garrulus glandarius*	-0.797
Sylvia curruca	2.893	*Phylloscopus trochilus*	-1.054
Sylvia borin	2.831	*Prunella modularis*	-1.055
Ficedula hypoleuca	2.284	*Passer domesticus*	-1.229
Streptopelia decaocto	2.208	*Emberiza citronella*	-1.277
Phylloscopus sibilatrix	2.123	*Falco tinnunculus*	-1.334
Regulus regulus	1.987	*Corvus frugilegus*	-1.438
Carduelis chloris	1.742	*Serinus serinus*	-1.524
Troglodytes troglodytes	1.572	*Pyrrhula pyrrhula*	-1.771
Alauda arvensis	1.218	*Picus viridis*	-1.849
Anas platyrhynchos	1.127	*Columba palumbus*	-1.964
Erithacus rubecula	0.986	*Turdus viscivoris*	-2.025
Parus palustris	0.862	*Sturnus vulgaris*	-2.148
Buteo buteo	0.607	*Coccothraustea coccothraustes*	-2.249
Phylloscopus collybita	0.522	*Columba oenas*	-2.329
Parus major	0.507	*Locustella naevia*	-2.348
Acrocephalus schoenobaenus	0.392	*Emberiza schoeniclus*	-2.438
Turdus philomelos	0.282	*Aegithalos caudatus*	-3.036
Dendrocopos major	0.272	*Corvus corax*	-3.328
Anthus pratensis	0.032	*Accipiter nisus*	-3.912
Saxicola rubetra	0.014	*Dendrocopos minor*	-3.953
Sylvia atricapilla	0.009	*Lanius collurio*	-4.693
		Corvus monedula	-7.384

An ANCOVA relating individual species CII slopes to the habitat preference, migratory status and mass of species indicated that, of these traits, only habitat preference was approaching significance to species CII at the 5% level (Table 4.3.3). This indicates that, based on the limited data available, these traits are not a key factor affecting the slope of individual species CIIs.

Table 4.3.3 ANCOVA relating species traits (habitat preference, migratory status or mass) to individual species CII slopes. The F value demonstrates what proportion of the variation (CII slope) is caused by each factor (environmental variable) (Df = degrees of freedom) at the 5% significance level. Residual Df=56.

Biological variable	Df	F	*p*
Habitat Preference	2	2.757	0.072
Migratory Status	2	1.993	0.145
Mass	1	0.053	0.819
Duration	1	0.364	0.549

4.4 Discussion

The observed patterns in regional and national CIIs (for those countries with ≥20 years of trend data) suggest that climatic change is having a large and measurable impact upon populations of common bird species across Europe.

National CIIs indicate that, for shorter runs of monitoring data (<15 years), there is little detectable signal of climate upon bird population trends (Figure 4.3.2, appendix 6.2). However, for longer runs of data (>20 years), there is a clear signal at a national level that bird population trends are responding to climatic change (Figure 4.3.1). These indicators of bird biodiversity at a national level suggest that the impacts of recent climatic change vary among European countries, probably resulting from the differing extent of those changes among countries.

Regional indicators also clearly show a link between the number of years of trend data available and the strength of the CII produced (Figure 4.3.3). Of the regional CIIs, only the southern European indicator demonstrates no impact of climatic change on the bird populations in southern Europe. This is the region with the lowest amount of trend data as, although the CII spans 19 years, only three countries make up the southern region trend; moreover, only one country (France) has trend data prior to 2000. This undermines confidence in the southern regional index as a reliable indicator of what has

been happening in southern Europe over the last 20 years. In contrast the monitoring periods covered by the northern European trend data, which is also made up of only three countries, cover the majority of this more extensive monitoring period.

Due to its location between the temperate climate of the mid-latitudes and the desert conditions of the subtropical high pressure belt, southern Europe is perceived by many to be more vulnerable to climatic change than other areas of Europe (Cubasch *et al.* 1996; Carter and Hulme 2000). Of the PECBMS species included in this analysis, more species were negatively affected in southern Europe than in north Europe (Figure 4.3.4).

Regional indicators show a particularly rapid increase in the past twenty years, coinciding with a period of rapid warming (Trenberth *et al.* 2007). This finding is similar to that of Gregory *et al.* (2009), who looked at bird population trends in relation to future projections. Here however, we looked at recent observed trends in relation to recent climatic change. The methods used to produce these CIIs closely followed those published by Gregory *et al.* (2009). The differences to Gregory *et al.*'s work includes the use of more than one SDM method (Gregory *et al.* only used CRS to produce their CII). Using more than one approach to model European bird distributions against climate acts to validate the results of the models, as similar results were produced by both modelling methods. Furthermore, the amount of species distribution data used during modelling was increased here to include breeding ranges in North Africa, Turkey and Cyprus, as well as updated climate scenario and emissions data.

The main development of this work, relative to that of Gregory *et al.* (2009), is to test the generality, at different spatial scales across Europe, of the finding that climatic warming is having a detectable effect on bird population trends across the continent. This development was prompted by the assumption that climatic effects will vary across Europe, which has been confirmed by this work (see Sections 4.3.1, 4.3.2). Many policy processes and levers operate at national scales. Therefore, downscaling the continent-wide findings is vital to enable the understanding of climatic change impacts at scales of relevance to policy responses.

The CIIs produced demonstrated evidence of negative as well as positive effects. Although countries with longer runs of bird population trend data demonstrated a clear relationship with climatic change, many countries (Table 4.3.1) and species (Figures 4.3.6 and 4.3.7) did not react as predicted to climatic change. Countries with short runs

of data may be influencing these trends and a more restricted analysis, including only countries with >20years of data, might provide more robust trends. Furthermore, the calculations of the CII does not take into account any differences that might exist between CST+ and CST- species in body mass, habitat preference and migratory status. Gregory *et al.* (2009) found that these biological traits were important factors in predicting population trend. However, they also found that the CII adjusted to take these variables into account followed a similar trajectory to the unadjusted version of the CII; therefore, producing CIIs which do not account for these biological traits does not present a significant concern. Furthermore, we found that none of the species traits we considered as potential covariates were significantly associated with species' CII slopes. There is a tendency for the CII slopes to be greater and more positive for long-distance migrants. This however, was not picked up by the ANCOVA.

Confounding factors can affect the ability to attribute changes in population trends specifically to climate. Clavero *et al.* (2011) suggest that indicator trends could be confounded by landscape scale land-use processes rather than climate. Spatially limited land-use changes could cause population changes to be incorrectly attributed to climate. For example, a species might be declining in the south of its range due to habitat loss and increasing in the north due to habitat creation/conservation; without considering land-use alterations, this pattern could be misinterpreted as being climate driven. Conversely, this could explain why many species are not responding as predicted to climatic change. For example, climate may be improving in Western Europe for a given species but population trends are not responding positively due to agricultural expansion. In the species' Eastern European range, the population may be increasing due to agricultural abandonment, despite a gradual decline in climatic suitability. The inclusion of some species whose populations are being strongly affected by processes other than climate may have confounded some results. For example, negative CII slopes for some raptor species (e.g. *Accipiter nisus* -3.912, *Falco tinnunculus* -1.334) may be due to persecution within climatically improving areas. Gregory *et al.* (2009) excluded population trends for two raptors whose population had been heavily influenced by pesticide poisoning in the 1950 – 60s, and continued human persecution. It would be interesting to re-examine both regional and national results omitting such species to see what effect this may have. It is however, important to note that there are factors other than climate which may dominate many species' dynamics. Aiming to consider all of

these factors would detract from one of the main aims of the CII, to provide a straightforward and easily updatable indicator.

Birds are good indicators of biodiversity due to their widespread, mobile, diverse, and easy to survey nature, as well as well established long term monitoring schemes (Blair 1999, Gregory *et al.* 2003, 2005, Butchart *et al.* 2010). It is difficult to construct indicators of the impact of climatic change upon other groups of species as long-term population monitoring data are lacking. The CII includes species of several threat categories (IUCN 2002), species occurring in different biomes, and species with ranges sizes of differing extents. As such, a wide range of species are covered and, as climatic change is shown significantly to impact upon bird population trends, it is expected that these species indicators may also inform population changes driven by climate in other taxa (Lindenmayer *et al.* 2000, Gregory *et al.* 2005, 2009). However, changes in dispersive taxa with short generation times might be expected to respond more rapidly to climatic changes than bird populations. For example, there are well documented rapid changes in the distribution of UK butterflies which have been attributed to climate and have occurred well in advance of any corresponding changes in taxa with lower reproductive rates and dispersal abilities (Willis *et al.* 2009). Birds, being neither strongly *r* nor *K* selected (Boyce 1979), and of intermediate trophic levels, might be considered a model species group to represent intermediate levels of response to longer term climatic change. Whilst *r*-selected, dispersive species provide better indicators of both short and long-term changes due to their rapid potential response rate (Western 2001).

National and regional level CIIs should be considered by policy makers as they can be used to track biological impacts on an annual basis (Gregory *et al.* 2009) and more accurately inform national decision making regarding policy responses. The proposed CIIs are relevant to policy makers because they can be used to track the biological impacts of climatic warming in near real-time, to set targets for the future level of the CIIs or their rate of change. Policy objectives based around these indicators may include stabilising the indicator, or at least slowing the rate of increase (Gregory *et al.* 2008, 2009, van Strien *et al.* 2009). Importantly, national and regional CIIs can serve to highlight changes due to climate that are masked by aggregating trends over larger spatial scales. The CIIs produced here are easily updated and can be calculated annually

using population data from European bird monitoring schemes. As most countries with long term trend data are in northern and western European countries, the CII trends for other regions currently contain greater uncertainty. The accuracy of indicators produced for regions with less data will increase as the number of years of monitoring increases (Hustings 1992, Kwak & Hustings 1994, Marchant *et al.* 1997). Here, we clearly show that CIIs are more effective when calculated using trend data from 20 years or longer (Table 4.3.1 and Figure 4.3.3), so continually collating sequential annual count data for use in these calculations would enable a clearer demonstration of the tracked impact of climatic change. The production of an easily updated national indictor has more relevance to policy makers than indicators produced on a wider scale and will therefore enable more accurate and measurable management plans to be produced and monitored.

4.5 References

Balmford, A., Bennun, L., Ten Brink, B., Cooper, D., Cote, I.M., Crane, P., Dobson, A., Dudley, N., Dutton, I., Green, R.E., Gregory, R.D., Harrison, J., Kennedy, E.T., Kremen, C., Leader-Williams, N., Lovejoy, T.E., Mace, G., May, R., Mayaux, P., Morling, P., Phillips, J., Redford, K., Ricketts, T.H., Rodriguez, J.P., Sanjayan, M., Schei, P.J., van Jaarsveld, A.S. and Walther, B.A. (2005) The convention on biological diversity's 2010 target. *Science* **307** 212-213

BirdLife International (2010) *Meeting the 2020 biodiversity targets: action and monitoring based on birds*. Cambridge, UK: BirdLife International

Blair, R.B. (1999) Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity. *Ecological Applications* **9** 164-170

Boyce, M.S. (1979) Seasonality and patterns of natural selection for life histories. *The American Naturalist* **114** 569-583

Burgess, J., Harrison, C.M. and Filius, P. (1999) Environmental communication and the cultural politics of environmental citizenship. *Environment and Planning A* **30** 1445-1460

Butchart, S.H.M., Walpole, M., Collen, B., Van Strien, A., Scharleman, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Daidson, N.C., Denter, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J-F., Leverington, F., Loh, M., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader,

S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vie, J-C. and Watson, R. (2010) Global biodiversity: indicators of recent declines. *Science* **328** 1164-1168

Carter, T.R. and Hulme, M. (2000) Key findings from the first ECLAT-2 workshop "Representing uncertainties in climate change scenarios and impact studies". In: J. Beersma, M. Agnew, D. Viner and M. Hulme (eds.). *Climate scenarios for water-related and coastal impacts*, ECLAT-2 Workshop Report No. 3, Climatic Research Unit, University of East Anglia, Norwich, UK, 10-14

Chernoff, H. and Lehmann E.L. (1954) The use of maximum likelihood estimates in χ^2 tests for goodness-of-fit. *The Annuals of Mathematical Statistics* **25** 579–586

Chiarucci, A., Bacaro, G. and Scheiner, S.M. (2011) Old and new challenges in using species diversity for assessing biodiversity. *Philosophical Transactions of the Royal Society: Biology* **366** 2426-2437

Clavero, M., Villero, D. and Brotons, L. (2011) Climate change or land use dynamics: do we know what climate change indicators indicate? *PLoS one* **6** e18581

Cubasch, U., von Storch, H., Waszkewitz, J. and Zorita, E. (1996) Estimates of climate change in southern Europe derived from dynamical climate model output. *Climate Research* **7** 129-149

Defra (2012) A strategy for England's wildlife and ecosystem services. Biodiversity 2020 indicators: 2012 Assessment. *Crown Copyright May 2012*

Doswald, N., Willis, S.G., Collingham, Y.C., Pain, D.J., Green, R.E. and Huntley, B. (2009) Potential impacts of climatic change on the breeding and non-breeding ranges and migration distance of European *Sylvia* warblers. *Journal of Biogeography* **36** 1194-1208

Duelli, P. and Obrist, M.K. (2003) Biodiversity indicators: the choice of values and measures. *Agriculture, Ecosystems and Environment* **98** 87-98

ESRI 2011. ArcGIS desktop: release 10. Redlands, California: Environmental Systems Research Institute

Government annual report (2001) Achieving a better quality of life. Review of progress towards sustainable development. *London: Department of the Environment, Transport and Regions*

Green, R.E., Collingham, Y.C., Willis, S.G., Gregory, R.D., Smith, K.W. and Huntley, B. (2008) Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters* **4** 599-602

Gregory, R.D., Noble, D., Field, R., Marchant, J., Raven, M. and Gibbons, D.W. (2003) Using birds as indicators of biodiversity. *Ornis Hungarica* **12-13** 11-24

Gregory, R.D., Noble, D.G. and Custance, J. (2004) The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis* **146 s2** 1-13

Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B. and Gibbons, D.W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society London B* **360** 269–288

Gregory, R.D., Vorisek, P., Noble, D.G., van Strien, A.J., Pazderová, A., Eaton, M.E., Gmelig., Meyling, A.W., Joys, A., Foppen, R.P.B. and Burfield, I.J. (2008) The generation and use of bird population indicators in Europe. *Bird Conservation International* **18** S223–S244

Gregory, R.D., Willis, S.G., Jiguet, F., Vorisek, P., Klvanova, A., van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D. And Green, R.E. (2009) An indicator of the impact of climatic change on European bird populations. *PloS one* **4** 1-6

Gregory, R.D and van Strien, A. (2010) Wild bird indicators: using composite population trends of birds as measures of environmental health. *Ornithological Science* **9** 3-22

Hansson, L. (1998) Nestedness as a conservation tool: plants and birds of oak–hazel woodland in Sweden. *Ecology Letters* **1** 142–145

Hustings, F. (1992) European monitoring studies on breeding birds: an update. *Bird Census News* **2** 1–56

IUCN (2002) *2002 IUCN Red List of threatened species.* Gland: IUCN www.redlist.org

Jones, J.P.G. (2011) Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology* **48** 9-13

Julliard, R., Jiguet, F. and Couvet, D. (2004) Evidence for the impact of global warming on the long-term population dynamics of common birds. **271** 490-492

Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D. and Lebrun, P. (2004) Testing the value of six taxonomic groups as biodiversity indicators at a local scale. *Conservation Biology* **18** 667-675

Kwak, R.G.M. and Hustings, M.F.H. (1994) *National common birds census projects in Europe: an overview.* In Hagemeijer, W. and Verstrael, T. (eds) *Bird numbers (1992) distribution, monitoring and ecological aspects. Proceedings 12th international conference of IBCC and EOAC:* 347–352. Statistics Netherlands, Voorburg & SOVON, Beek-Ubbergen, Netherlands

Landres, P.B., Verner, J. and Thomas, J.W. (1988) Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* **2** 316-328

Lindenmayer, D.B., Margules, C.R. and Botkin, D.B. (2000) Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology* **14** 941-950

Mace, G.M. and Baille, J.E.M. (2007) The 2010 biodiversity indicators: challenges for science and policy. *Conservation Biology* **21** 1406-1413

Marchant, J.H., Forest, C. and Greenwood, J.J.D. (1997) A review of large-scale generic population monitoring schemes in Europe. *Bird Census News* **2** 42–80

Nichols, J.D. and Williams, B.K. (2006) Monitoring for conservation. *Trends in Ecology and Evolution* **21** 668-673

Parmesan, C. and Yohe, G., (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421** 37-42

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. and Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421** 57-60

Schiller, A., Hunsaker, C.T., Kane, M.A., Wolfe, A.K., Dale, V.H., Suter, G.W., Russell, C.S., Pion, G., Jensen, M.H. and Konar, V.C. (2001) Communicating ecological indicators to decision makers and the public. *Conservation Ecology* **5** 19

Thiollay, J-M. (1997) Disturbance, selective logging and bird diversity: a Neotropical forest study. *Biodiversity and Conservation* **6** 115-1173

Torti, V.M. and Dunn, P.O. (2005) Variable effects of climate change on six species of North American birds. *Oecologia* **145** 486-495

Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Klein Tank, A., Parker, D., Rahimzadeh, F., Renwick, J.A., Rusticucci, M., Soden, O. and Zhai P. (2007) *Observations: surface and atmospheric climate change.* In: Climate change 2007: the physical science basis. Contribution of working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L. (eds.)]. *Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA* 235-336

Van Strien, A.J., van Duuren, L., Foppen, R.P.B. and Soldaat, L.L. (2009) A typology of indicators of biodiversity change as a tool to make better indicators. *Ecological Indicators* **9** 1041-1048

Walther, G-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J-M., Hoegh-Guldberg, O. and Bairlein, F. (2002) Ecological responses to recent climate change. *Nature* **416** 389-395

Western, D. (2001) Human-modified ecosystems and future evolution. *Proceedings of the National Academy of Sciences of the United States of America* **98** 5458-5465

Willis, S.G., Hill, J.K., Thomas, C.D., Roy, D.B., Fox, R., Blakeley, D.S. and Huntley, B. (2009) Assisted colonization in a changing climate: a test-study using two U.K. butterflies. *Conservation Letters* **2** 45-51

Chapter 5 – Synthesis and Discussion

Recent, anthropogenic climatic change is having a considerable impact upon population trends and levels of biodiversity (IPCC 2007, McCarty 2001, Root *et al.* 2003, Stenseth *et al.* 2002, Torti and Dunn 2005). Climatic change also reduces ecosystem functioning, with a knock on effect of reducing biodiversity (Leemans and Eickhout 2004).

Current and predicted levels of climatic change represent unprecedented challenges for the management of biological conservation (Stern 2007). Therefore, policy makers are looking increasingly to modelled projections of species' distributions under future climates to inform conservation policy, invasive species management and disease control measures (Beale and Lennon 2012). Many species are struggling to adapt to recent climatic change as, not only is it more rapid than previous changes (IPCC 2007), but species are under increasing pressure from other human practices such as intensive agriculture and urbanisation, land drainage, fertilizer usage and land abandonment (Bouma *et al.* 1998). The long-term trend for the past 500 million years has been towards greater diversity. However, the current rate of extinctions is suggested to be 100 to 1000 times greater than the natural rate, and is accelerating (May *et al.* 1995). This extinction rate can be expected to accelerate further if the pressures from the main drivers of biodiversity loss are not reduced. The accelerating extinction of species is the tip of the iceberg for global wildlife declines that threaten to disrupt vital ecosystem processes and services (Şekercioğlu *et al.* 2004). To quantify biodiversity fully is too intricate and complex a process to be undertaken regularly in order to inform policy. Therefore, biodiversity is characterised through the use of surrogate measures such as biodiversity indicators. Biodiversity measurement is needed due to the widespread concern of the loss of biodiversity and the need for policy responses to this to be effective. Therefore, this thesis aimed to produce indicators of the impact of climatic change on downscaled levels of biodiversity by using population data from European breeding birds to act as a proxy for national and regional ecosystem health and to indicate trends in levels of biodiversity at these scales (Walther *et al.* 2002, Strode 2003, Gregory *et al.* 2005, Hitch and Leberg 2007).

The reliability of predictions of population trends relies strongly upon the modelling technique used (Thuiller 2003). The initial section of this thesis, which looked at the accuracy of three methods of species distribution modelling (SDM) (CRS, GAM and

MaxEnt), provided an essential foundation for the rest of the research. The successful utilization of an indicator relies heavily upon accurate predictions of how population trends are shifting in response to global climatic change, to inform conservation policy (Araújo *et al.* 2005, Beale *et al.* 2006). It is widely acknowledged that significant levels of variability exist within the projections of SDMs and that assessment of model performance is crucial (Mouton *et al.* 2010) as SDMs are only useful if they are robust (Guisan and Thuiller 2005). This acknowledgement validates the subsequent work of producing climate suitability trends (CSTs), to define the most appropriate modelling techniques and data sets.

Chapter 2 demonstrated, through the use of past distribution data, that the inclusion of species distribution data from North Africa, Turkey and Cyprus, in addition to the data in the Climatic Atlas of European Breeding Birds (Huntley *et al.* 2007), improved SDM predictions of population trends. Furthermore, the presence only model (MaxEnt) had less accurate predictive capabilities than the other SDMs considered (GAM (generalised additive model) and CRS (climate response surface)) of which CRS outperformed GAMs. On the basis of those findings, both CRS and GAM modelling methods were used to produce an indicator of the impacts of climatic change on levels of biodiversity.

The initial step towards producing a CII, using the European breeding bird population data provided by the Pan European Bird Monitoring Scheme (PECBMS), was to produce and investigate climate suitability trends (CSTs). The PECMBS trend data was compared to climatic suitability in order to investigate the use of climatic change as a predictor of population trends. Further variables were also considered to determine their effect on this analysis; these variables included monitoring duration and the size of country being analysed, as well as species' biological traits (habitat preference, life history and migratory status). At both national and individual species levels, PECBMS trends were not consistently significantly related to CST trends. The national results revealed important variations in trends between countries and indicated that other factors may be more important than climate in affecting and constraining species' populations. Importantly, the results suggested a detectable climate signal in the population trends within individual countries. The information gleaned from this analysis was then implemented to produce CII.

CIIs were produced at three different scales to relate population trends to climatic suitability: regional, national and individual species levels. Within an area, CIIs indicate the divergence in population trends between species predicted by climatic envelope models to be favourably affected by climatic change, and those predicted to be adversely affected. At a species level, CIIs indicate the direction and rate of population changes across all countries.

Climate is having a detectable effect upon populations of common breeding bird species across Europe, especially over the past 20 years, which coincides strongly with a period of rapid warming (Trenberth *et al.* 2007). Unsurprisingly, perhaps, this pattern appears to be stronger in both countries and regions with longer population data sets. Furthermore, the impacts of climatic change vary among the European regions investigated; this may be due (as expected) to spatial variation in the extent of recent climatic change. The investigation into individual species' CIIs demonstrated evidence of a mixture of negative and positive effects, with none of the species' biological traits significantly affecting species' CII slopes. This lack of a clear outcome demonstrates that the relationship between climatic change and individual species' population trends requires further investigation to determine the mechanisms impacting upon this relationship.

The scope of this study precluded ensemble forecasting of the data. Ensemble forecasting involves the use of several models in one study and examining the results in a way which enables combination of each of the model outcomes (Araújo *et al.* 2005, Araújo and New 2007). This may have improved the reliability of the SDM results as different SDM techniques have been demonstrated to provide very different results for data sets of the same species and to vary widely across species (Thuiller 2003). It has been demonstrated throughout this work that pressures other than climate, which we have not had the time to consider fully in this study, have an impact upon population trends i.e. exploitation, land management processes, biological invasions (Butchart *et al.* 2010, Clavero *et al*. 2011).

There are many opportunities to build on the work presented in this thesis. One area of analysis which has not been explicitly covered is the incorporation of the effects of climatic change at breeding and non-breeding grounds, both individually and as a whole, to discover which of these sites most affects phenology advancements and

climate suitability and how this, in turn, affects the production of CIIs. Doswald *et al.* (2009) suggested that breeding grounds, non-breeding grounds and migratory status each affect how climate impacts bird species. Therefore, separate indicators could be produced for each of these groupings on national and regional scales to investigate these differences further. Additionally, the number of species used for this analysis was limited to those widespread species monitored by the PECBMS. It is possible that indicators would show even more marked trends if the availability of good quality count data extended to all bird species that breed in Europe (Gregory *et al.* 2009). A further interesting extension would be the implementation of this project across all countries rather than limiting it to Europe.

When compared to many areas of the world, especially the tropics, biodiversity in Europe is relatively low in overall richness (Steiger 2005); therefore, extending this work globally would give much more insight into managing the overall biodiversity of species and habitats. However, comparable levels of monitoring data used in this thesis are not available for the tropics. There are few climate change studies of the effects on the bird communities of entire tropical forest regions (Harris et al., 2011), and few tropical bird families have been assessed in their entirety (Sekercioglu *et al.* 2012). Most tropical bird species vulnerable to climate change are not currently considered threatened with extinction, due to lack of knowledge. Increasingly the importance of theses areas and how prone to extinction these species may be, is being realised (La Sorte and Jetz 2010; Harris *et al.* 2011; Sodhi *et al.* 2011; Wormworth and Sekercioglu 2011). Establishing and maintaining locally based, long-term tropical bird monitoring may prove essential to help protect birds against climate change. Therefore the gathering of information on the ecology, and current and future distributions of these species is an urgent priority.

Due to the documented widespread loss of biodiversity, quantifying levels of biodiversity is necessary to communicate complex processes in a simple manner, to enable a well informed policy response. The scale of response to climatic change is dependent upon many distinct, individualistic factors; these include habitat, population and species concerned, as well as heterogeneous changes in temperature and precipitation (Walther *et al*. 2002). Therefore, the implications of this investigation into the effect of climatic change at sub-European levels provides support for monitoring to be undertaken of regional ecosystem biodiversity. Furthermore, validating each step of

the process of creating a climatic impact indicator provides a more truthful indication of how climatic change is affecting global biodiversity.

The future implications of climatic change necessitate more precise means of simulating population responses and the effect, therefore, of predicted climatic change on global biodiversity. Indicator species are no substitute for detailed knowledge of ecological process or individual species' responses; such knowledge is essential in order to assess fully the causes of changes in both population trend and levels of biodiversity and in formulating a response to such changes (Bibby 1999, Gregory *et al.* 2005). However, indicators are generally viewed as a powerful tool to enable complex scientific information to be communicated clearly to policy makers (Gregory *et al.* 2005).

5.2 References

Araújo, M.B., Pearson, R.G., Thuiller, W. and Erhard, M. (2005) Validation of species-climate impact models under climate change. *Global Change Biology* **11** 1504-1513

Araújo, M.B. and New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution* **22** 42-47

Beale, C.M., Burfield, I.J., Sim, I.M.W., Rebecca, G.W., Pearce-Higgins, J.W. and Grant, M.C. (2006) Climate change may account for the decline in British ring ouzels *Turdus torquatus. Journal of Animal Ecology* **75** 826-835

Beale, C.M. and Lennon, J.J. (2012) Incorporating uncertainty in predictive species distribution modelling. *Philosophical Transactions of the Royal Society: Biological Sciences* **367** 247-258

Bibby, C.J. (1999) *Making the most of birds as environmental indicators.* In: Adams, N.J. & Slotow, R.H. (eds) Proc. 22 International Ornithological Congregation, Durban. Ostrich **70** 81–88

Bouma, J., Varallyay, G. and Batjes, N.H. (1998) Principal land use changes anticipated in Europe. *Agriculture, Ecosystems and Environment* **67** 103-119

Burgess, J., Harrison, C.M. and Filius, P. (1999) Environmental communication and the cultural politics of environmental citizenship. *Environment and Planning A* **30** 1445-1460

Butchart, S.H.M., Walpole, M., Collen, B., Van Strien, A., Scharleman, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter,

K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Daidson, N.C., Denter, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J-F., Leverington, F., Loh, M., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vie, J-C. and Watson, R. (2010) Global biodiversity: indicators of recent declines. *Science* **328** 1164-1168

Clavero, M., Villero, D. and Brotons, L. (2011) Climate change or land use dynamics: do we know what climate change indicators indicate? *PLoS one* **6** e18581

Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B. and Gibbons, D.W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **360** 269–288

Gregory, R.D., Willis, S.G., Jiguet, F., Vorisek, P., Klvanova, A., van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D. And Green, R.E. (2009) An indicator of the impact of climatic change on european bird populations. *PloS one* **4** 1-6

Guisan, A. and Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling* **135** 147–186

Harris, J.B.C., Sekercioglu, Ç.H., Sodhi, N.S., Fordham, D.A., Paton, D.C. and Brook, B.W. (2011). The tropical frontier in avian climate impact research. *Ibis* **153** 877–882

Hitch, A.T. and Leberg, P.L. (2007) Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology* **21** 534-539

Huntley, B., Green, R. E., Collingham, Y. and Willis, S. G. (2007). *A climatic atlas of European breeding birds*. Durham, Sandy and Barcelona: Durham University, RSPB and Lynx Editions

IPCC (2007) Climate change 2007: synthesis report. Contribution of working groups I, II and III to the Fourth Assessment. *Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, Pachauri, R.K and Reisinger, A.(eds.)]. IPCC, Geneva, Switzerland, 104

IUCN (2012) About biodiversity - *What is biodiversity?* www.iucn.org - Accessed 07/05/2012

La Sorte, F.A. and Jetz, W. (2010) Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences* **277** 3401–3410

McCarty, J.P. (2001) Ecological consequences of recent climate change. *Conservation Biology* **15** 320-331

Mouton, A.M., De Baets, B. and Goethals, P.L.M. (2010) Ecological relevance of performance criteria for species distribution models. *Ecological Modelling* **221** 1995-2002

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. and Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421** 57-60

Schiller, A., Hunsaker, C.T., Kane, M.A., Wolfe, A.K., Dale, V.H., Suter, G.W., Russell, C.S., Pion, G., Jensen, M.H. and Konar, V.C. (2001) Communicating ecological indicators to decision makers and the public. *Conservation Ecology* **5** 19

Sekercioglu, C.H., Primack, R.B. and Wormworth, J. (2012) The Effects of Climate Change on Tropical Birds. *Biological Conservation* **148** 1-18

Sekercioglu, C.H., Schneider, S.H., Fay, J.P. and Loarie, S.R. (2008) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* **22** 140-150

Sodhi, N.S., Sekercioglu, Ç.H., Robinson, S. and Barlow, J. (2011) *Conservation of tropical birds.* Wiley-Blackwell, Oxford

Steiger, F. (2005) *A user's guide to biodiversity indicators*. European Academies Science Advisory Council. The Royal Society

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K-S. and Lima, M. (2002) Review: ecological effects of climate fluctuations. *Science* **297** 1292-1296

Stern, N. (2007) *Stern Review: The Economics of Climate Change*. Cambridge University Press, Cambridge

Strode, P.K. (2003) Implications of climate change for North American wood warblers (Parulidae). *Global Change Biology* **9** 1137-1144

Thuiller, W. (2003) BIOMOD- optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology* **9** 1353-1362

Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Klein Tank, A., Parker, D., Rahimzadeh, F., Renwick, J.A., Rusticucci, M., Soden, O. and Zhai,

P. (2007) *Observations: surface and atmospheric climate change.* In: Climate change 2007: the physical science basis. Contribution of working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L. (eds.)]. *Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA* 235-336

Torti, V.M. and Dunn, P.O. (2005) Variable effects of climate change on six species of North American birds. *Oecologia* **145** 486-495

Walther, G-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J-M., Hoegh-Guldberg, O. and Bairlein, F. (2002) Ecological responses to recent climate change. *Nature* **416** 389-395

Wormworth, J. and Sekercioglu, Ç.H. (2011) *Winged sentinels: birds and climate change*. Cambridge University Press, Cambridge

6 Appendix

Table 6.1 A list of species, for which PECBMS trend data was available, used in this study, including biological traits (see 3.2.3): LDM=Long Distance Migrant, R=Resident, SDM=Short Distance Migrant. **Bold** = those species used in the final calculation of CST (PECBMS trend data ≥18 years).

Species	Habitat Preference	Broad Migratory Status	Mass (ln)
Acrocephalus arundinaceus	**Other**	**LDM**	**3.303**
Acrocephalus palustris	**Other**	**LDM**	**2.477**
Acrocephalus schoenobaenus	**Other**	**LDM**	**2.416**
Acrocephalus scirpaceus	**Other**	**LDM**	**2.510**
Carduelis cannabina	**Farmland**	**SDM**	**2.728**
Carduelis carduelis	**Other**	**SDM**	**2.747**
Carduelis chloris	**Other**	**SDM**	**3.325**
Carduelis flammea	**Other**	**SDM**	**2.565**
Carduelis spinus	**Woodland**	**SDM**	**2.674**
Oenanthe hispanica	Farmland	LDM	2.674
Phoenicurus ochruros	**Other**	**SDM**	**2.803**
Oenanthe oenanthe	**Other**	**SDM**	**3.105**
Phoenicurus phoenicurus	**Woodland**	**LDM**	**2.674**
Saxicola rubetra	**Farmland**	**LDM**	**2.809**
Saxicola torquata	**Farmland**	**SDM**	**2.728**
Merops apiaster	**Other**	**LDM**	**4.036**
Upupa epops	**Farmland**	**LDM**	**4.117**
Jynx torquill	**Other**	**LDM**	**3.512**
Certhia brachydactyla	**Woodland**	**R**	**2.140**
Sitta europaea	**Woodland**	**R**	**3.091**
Certhia familiaris	**Woodland**	**R**	**2.197**
Nucifraga caryocatactes	**Woodland**	**R**	**5.130**
Corvus corone	**Other**	**R**	**6.346**
Cyanopica cyanus	Woodland	R	4.277
Corvus frugilegus	**Farmland**	**SDM**	**6.190**
Garrulus glandarius	**Woodland**	**R**	**5.081**
Corvus monedula	**Other**	**SDM**	**5.505**
Pica pica	**Other**	**R**	**5.112**
Pyrrhocorax pyrrhocorax	Woodland	R	5.112
Corvus corax	**Other**	**R**	**7.054**
Cuculus canorus	**Other**	**LDM**	**4.727**
Streptopelia decaocto	**Other**	**R**	**4.984**
Columba oenas	**Woodland**	**SDM**	**5.635**
Columba palumbus	**Other**	**SDM**	**6.194**
Streptopelia turtur	**Farmland**	**LDM**	**4.883**
Anas platyrhynchos	**Other**	**SDM**	**6.987**
Emberiza cia	Other	SDM	3.219

Table 6.1 Continued

Species	Habitat Preference	Broad Migratory Status	Mass (ln)
Emberiza cirlus	Farmland	R	3.120
Emberiza citrinella	**Farmland**	**SDM**	**3.277**
Emberiza hortulana	**Farmland**	**LDM**	**3.170**
Emberiza melanocephala	Farmland	LDM	3.170
Emberiza rustica	**Woodland**	**LDM**	**3.144**
Emberiza schoeniclus	**Other**	**SDM**	**2.907**
Miliaria calandra	**Farmland**	**SDM**	**4.047**
Coccothraustea coccothraaustes	**Woodland**	**SDM**	**3.989**
Fringilla coelebs	**Other**	**SDM**	**3.020**
Carpodacus erythrinus	**Other**	**LDM**	**3.182**
Fringilla montifrigilla	**Other**	**SDM**	**3.182**
Pyrrhula pyrrhula	**Other**	**SDM**	**3.082**
Serinus serinus	**Farmland**	**SDM**	**2.416**
Ficedula albicollis	**Woodland**	**LDM**	**2.332**
Aegithalos caudatus	**Other**	**R**	**2.104**
Ficedula hypoleuca	**Woodland**	**LDM**	**2.451**
Regulus ignicapillus	**Woodland**	**SDM**	**1.723**
Regulus regulus	**Woodland**	**SDM**	**1.740**
Muscicapa striata	**Other**	**LDM**	**2.681**
Bonasa bonasia	**Woodland**	**R**	**6.061**
Perdix perdix	**Farmland**	**R**	**5.943**
Limosa limosa	**Farmland**	**SDM**	**5.728**
Numenius phaeopus	**Other**	**LDM**	**6.001**
Tringa totanus	**Other**	**SDM**	**4.860**
Ardea cinerea	**Other**	**SDM**	**7.274**
Lullula arborea	**Other**	**SDM**	**3.292**
Alauda arvensis	**Farmland**	**SDM**	**3.616**
Calandrella brachydactyla	Farmland	LDM	3.616
Melanocorypha calandra	**Farmland**	**SDM**	**3.135**
Galerida cristata	**Farmland**	**R**	**3.735**
Galerida theklae	Woodland	R	3.597
Parus ater	**Woodland**	**R**	**2.208**
Parus caeruleus	**Other**	**R**	**2.588**
Parus cristatus	**Woodland**	**R**	**2.322**
Parus major	**Other**	**R**	**2.944**
Parus montanus	**Woodland**	**R**	**2.322**
Parus palustris	**Woodland**	**R**	**2.361**
Picus canus	**Woodland**	**R**	**4.920**
Dendrocopos major	**Other**	**R**	**4.402**
Dryocopus martius	**Woodland**	**R**	**5.771**
Dendrocopos medius	**Woodland**	**R**	**4.078**
Dendrocopos minor	**Woodland**	**R**	**2.986**
Dendrocopos syriacus	Woodland	R	4.376
Picus viridis	**Other**	**R**	**5.170**
Phylloscopus bonelli	**Woodland**	**LDM**	**2.186**

Table 6.1 Continued

Species	Habitat Preference	Broad Migratory Status	Mass (ln)
Phylloscopus collybita	**Woodland**	**SDM**	**2.015**
Phylloscopus sibilatrix	**Woodland**	**LDM**	**2.104**
Phylloscopus trochiloides	**Other**	**LDM**	**2.163**
Anthus campestris	Farmland	LDM	3.332
Anthus pratensis	**Farmland**	**SDM**	**2.912**
Anthus trivialis	**Woodland**	**LDM**	**3.223**
Pluvialis apricaria	**Other**	**SDM**	**5.366**
Vanellus vanellus	**Farmland**	**SDM**	**5.421**
Fulica atra	**Other**	**SDM**	**6.621**
Gallinula chloropus	**Other**	**SDM**	**5.580**
Buteo buteo	**Other**	**SDM**	**6.876**
Falco tinnunculus	**Farmland**	**SDM**	**5.380**
Circus aeruginosus	**Other**	**SDM**	**6.637**
Accipiter nisus	**Other**	**SDM**	**5.481**
Tringa glareola	**Other**	**SDM**	**4.290**
Actitis hypoleucos	**Other**	**SDM**	**3.945**
Tringa ochropus	**Woodland**	**SDM**	**4.268**
Burhinus oedicnemus	Farmland	SDM	6.133
Lanius collurio	**Farmland**	**LDM**	**3.398**
Lanius minor	Farmland	LDM	3.884
Oriolus oriolus	**Other**	**LDM**	**4.369**
Lanius senator	Farmland	LDM	3.555
Gallinago gallinago	**Other**	**SDM**	**4.754**
Passer domesticus	**Other**	**R**	**3.311**
Passer montanus	**Farmland**	**SDM**	**3.091**
Petronia petronia	Farmland	R	3.418
Sturnus unicolor	Farmland	R	4.508
Sturnus vulgaris	**Farmland**	**SDM**	**4.381**
Ciconia ciconia	**Farmland**	**LDM**	**8.153**
Ptyonoprogne rupestris	Other	SDM	3.157
Hirundo rustica	**Farmland**	**LDM**	**2.760**
Delichon urbica	**Other**	**LDM**	**2.674**
Cygnus olor	**Other**	**SDM**	**9.177**
Apus apus	**Other**	**LDM**	**3.627**
Sylvia atricapilla	**Other**	**SDM**	**2.741**
Sylvia borin	**Other**	**LDM**	**2.632**
Sylvia cantillata	**Other**	**LDM**	**2.380**
Sylvia communis	**Farmland**	**LDM**	**2.674**
Sylvia curruca	**Other**	**LDM**	**2.313**
Sylvia hortensis	**Other**	**LDM**	**3.100**
Sylvia melanocephala	**Other**	**SDM**	**2.425**
Sylvia nisoria	**Other**	**LDM**	**3.127**
Sylvia undata	Other	R	2.251
Turdus iliacus	**Other**	**SDM**	**4.114**
Turdus merula	**Other**	**SDM**	**4.727**

Table 6.1 Continued

Species	Habitat Preference	Broad Migratory Status	Mass (ln)
Turdus philomelos	**Other**	**SDM**	**4.199**
Turdus pilaris	**Other**	**SDM**	**4.644**
Turdus viscivoris	**Woodland**	**SDM**	**4.745**
Motacilla alba	**Other**	**SDM**	**3.045**
Motacilla cinerea	**Other**	**SDM**	**2.845**
Motacilla flava	**Farmland**	**LDM**	**2.632**
Bombycilla garrulus	**Woodland**	**SDM**	**4.032**
Cettia cetti	**Other**	**R**	**2.534**
Locustella fluviatilis	**Other**	**LDM**	**2.896**
Hippolais icterina	**Other**	**LDM**	**2.681**
Cisticola juncidis	Other	R	2.303
Locustella naevia	**Other**	**LDM**	**2.588**
Hippolais polyglotta	**Other**	**LDM**	**2.398**
Luscinia luscinia	**Other**	**LDM**	**3.170**
Luscinia megarhynchos	**Other**	**LDM**	**2.907**
Prunella modularis	**Other**	**SDM**	**2.981**
Erithacus rubecula	**Other**	**SDM**	**2.901**
Troglodytes troglodytes	**Other**	**SDM**	**2.186**

Table 6.2 Summary statistics for the relationship between CST and PECBMS for individual species. **Bold** = those species with a significant positive correlation. r= Pearson's correlation coefficient (between -1 and 1), p= probability the current result would have been found if the correlation coefficient were zero (null hypothesis). If $p<0.05$ the correlation coefficient is statistically significant. Only showing data from the 109 species present in two or more countries.

Species	CSTCRS v PECBMS Trend		GAMCRS v PECBMS Trend	
	r	p	r	p
Acrocephalus arundinaceus	-0.004	0.991	-0.116	0.749
Acrocephalus palustris	-0.038	0.893	0.124	0.659
Acrocephalus schoenobaenus	0.004	0.989	-0.072	0.815
Acrocephalus scirpaceus	0.003	0.992	0.043	0.888
Carduelis cannabina	0.030	0.907	0.217	0.402
Carduelis carduelis	-0.246	0.339	-0.264	0.304
Carduelis chloris	-0.077	0.076	0.089	0.718
Carduelis flammea	0.290	0.383	0.292	0.379
Carduelis spinus	-0.200	0.531	0.206	0.519
Phoenicurus ochruros	0.301	0.365	-0.298	0.365
Oenanthe oenanthe	-0.543	0.028	-0.300	0.256
Phoenicurus phoenicurus	0.501	0.046	0.438	0.087
Saxicola rubetra	-0.172	0.509	-0.151	0.563
Saxicola torquata	0.184	0.565	-0.083	0.796
Merops apiaster	-0.229	0.654	-0.901	0.006
Jynx torquilla	-0.695	0.005	-0.054	0.853
Certhia brachydactyla	0.336	0.308	-0.053	0.877

Table 6.2 Continued

Species	CSTCRS v PECBMS Trend		GAMCRS v PECBMS Trend	
	r	p	r	p
Sitta europaea	-0.244	0.360	-0.412	0.111
Certhia familiaris	-0.126	0.666	-0.354	0.211
Nucifraga caryocatactes	0.544	0.244	-0.164	0.751
Corvus corone	0.477	0.038	-0.084	0.732
Corvus frugilegus	-0.184	0.566	0.228	0.473
Garrulus glandarius	0.641	0.005	0.208	0.422
Corvus monedula	-0.125	0.633	-0.169	0.516
Pica pica	0.013	0.954	-0.030	0.899
Corvus corax	-0.127	0.639	0.059	0.828
Cuculus canorus	0.055	0.824	0.188	0.440
Streptopelia decaocto	-0.138	0.623	-0.091	0.747
Columba oenas	0.257	0.353	-0.074	0.793
Columba palumbus	-0.053	0.828	0.218	0.369
Streptopelia turtur	-0.579	0.028	0.663	0.008
Anas platyrhynchos	0.113	0.676	0.405	0.117
Emberiza citronella	0.301	0.209	0.207	0.394
Emberiza hortulana	-0.712	0.057	0.140	0.761
Emberiza schoeniclus	0.191	0.494	-0.214	0.443
Miliaria calandra	0.371	0.284	0.098	0.787
Coccothraustes coccothraustes	0.216	0.456	-0.515	0.056
Fringilla coelebs	-0.063	0.805	-0.136	0.589
Carpodacus erythrinus	-0.244	0.632	0.042	0.936
Pyrrhula pyrrhula	0.268	0.296	0.050	0.847
Serinus serinus	0.529	0.088	-0.027	0.937
Aegithalos caudatus	-0.431	0.082	-0.113	0.665
Ficedula hypoleuca	-0.105	0.744	-0.463	0.124
Regulus ignicapilla	-0.165	0.647	-0.055	0.879
Regulus regulus	-0.238	0.355	0.191	0.460
Muscicapa striata	-0.384	0.114	0.212	0.398
Bonasa bonasia	0.295	0.685	0.954	0.011
Perdix perdix	-0.364	0.163	-0.215	0.423
Tringa tetanus	-0.079	0.839	-0.205	0.593
Ardea cinerea	0.378	0.161	-0.109	0.697
Lullula arborea	0.082	0.810	0.479	0.130
Alauda arvensis	0.401	0.087	0.238	0.325
Galerida cristata	0.212	0.610	-0.260	0.528
Parus ater	0.423	0.078	-0.334	0.173
Parus caeruleus	0.056	0.823	0.596	0.008
Parus cristatus	0.086	0.761	0.170	0.543
Parus major	0.159	0.528	-0.270	0.277
Parus montanus	0.061	0.875	0.411	0.263
Parus palustris	-0.345	0.357	0.257	0.500

Table 6.2 Continued

Species	CSTCRS v PECBMS Trend		GAMCRS v PECBMS Trend	
	r	p	r	p
Dendrocopos major	-0.540	0.100	0.436	0.200
Dryocopus martius	0.050	0.897	-0.195	0.612
Dendrocopos medius	0.414	0.680	-0.119	0.912
Dendrocopos minor	-0.227	0.584	0.261	0.527
Picus viridis	-0.685	0.035	0.691	0.032
Phylloscopus collybita	0.136	0.706	-0.423	0.217
Phylloscopus sibilatrix	0.553	0.090	0.689	0.023
Phylloscopus trochiloides	0.298	0.398	0.436	0.201
Anthus pratensis	0.455	0.179	0.179	0.617
Anthus trivialis	0.136	0.706	-0.213	0.552
Vanellus vanellus	0.318	0.398	0.195	0.611
Fulica atra	-0.238	0.689	0.490	0.375
Gallinula chloropus	0.224	0.624	-0.756	0.036
Buteo buteo	0.261	0.493	0.501	0.160
Falco tinnunculus	0.240	0.561	-0.164	0.694
Circus aeruginosus	0.127	0.834	0.166	0.187
Accipiter nisus	-0.314	0.442	0.371	0.356
Tringa glareola	0.980	0.016	0.743	0.348
Actitis hypoleucos	0.146	0.844	0.051	0.946
Lanius collurio	-0.437	0.230	0.139	0.719
Oriolus oriolus	0.871	0.005	0.474	0.267
Gallinago gallinago	0.339	0.447	0.101	0.827
Passer domesticus	-0.075	0.846	-0.635	0.057
Passer montanus	0.106	0.785	0.155	0.688
Sturnus vulgaris	-0.314	0.372	0.564	0.082
Hirundo rustica	0.755	0.009	0.033	0.927
Delichon urbica	0.300	0.427	0.133	0.730
Cygnus olor	0.029	0.956	0.351	0.481
Apus apus	0.094	0.822	0.234	0.571
Sylvia atricapilla	0.415	0.227	0.335	0.338
Sylvia borin	0.353	0.311	-0.525	0.112
Sylvia communis	0.416	0.225	0.570	0.078
Sylvia curruca	0.456	0.178	-0.113	0.754
Sylvia nisoria	-0.931	0.084	0.323	0.755
Turdus iliacus	-0.989	0.007	-0.192	0.858
Turdus merula	0.502	0.131	0.183	0.610
Turdus philomelos	0.206	0.565	-0.108	0.765
Turdus pilaris	0.462	0.283	0.263	0.562
Turdus viscivorus	0.013	0.971	-0.255	0.472
Motacilla alba	0.445	0.303	0.023	0.961
Motacilla cinerea	0.350	0.545	0.352	0.543
Motacilla flava	0.589	0.086	0.056	0.885

Table 6.2 Continued

Species	CSTCRS v PECBMS Trend		GAMCRS v PECBMS Trend	
	r	p	r	p
Locustella fluviatilis	0.373	0.714	0.327	0.631
Hippolais icterina	0.716	0.112	0.117	0.894
Locustella naevia	-0.120	0.774	-0.097	0.817
Luscinia luscinia	0.408	0.473	0.866	0.030
Luscinia megarhynchos	0.542	0.244	0.320	0.525
Prunella modularis	0.244	0.493	-0.058	0.873
Erithacus rubecula	0.157	0.663	0.188	0.145
Troglodytes troglodytes	0.011	0.977	-0.243	0.494